

Mistaken Identities: On the Discodorididae Genera *Hoplodoris* Bergh, 1880 and *Carminodoris* Bergh, 1889 (Opisthobranchia, Nudibranchia)

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The phylogenetic status of the two discodoridid genera *Hoplodoris* and *Carminodoris* has been uncertain due to the lack of distinguishing generic features and lack of complete anatomical descriptions. Recent examination of discodoridid specimens from the type localities provides further anatomical detail that allows for a comparison of the two genera. There are few morphological characters that can be used to justify two distinct genera. Analyses indicate that the genus *Carminodoris* is a junior synonym of *Hoplodoris*. *Hoplodoris desmoparypha* Bergh, 1880, *C. mauritiana* Bergh, 1891 and *C. grandiflora* (Pease, 1860) are conspecific with *H. grandiflora* having priority. *Hoplodoris novaezelandiae* (Bergh, 1904) and *H. nodulosa* (Angas, 1864) are conspecific. *Carminodoris nodulosa*, misidentified by Kay and Young, 1969 from Hawaii, and *Carminodoris bifurcata* Baba, 1993 are conspecific and quite distinct from other species of *Hoplodoris*. *Hoplodoris armata* (Baba, 1993), *H. bifurcata* (Baba, 1993), *H. estrelyado* Gosliner and Behrens, 1998, *H. grandiflora* (Pease, 1860) and *H. nodulosa* (Angas, 1864) are valid species. Additionally, *Geitodoris* is closely related to *Hoplodoris* but more basally situated than *Hoplodoris*. Important diagnostic morphological characters of *Hoplodoris* that have been inherited from a common ancestor include penial hooks and denticulate radular teeth. Two new species of *Hoplodoris* are described. *Hoplodoris flammea* sp. nov. is known from Bali, Indonesia and *Hoplodoris bramale* sp. nov. is from the Pacific coast of Costa Rica, the latter representing the first record of *Hoplodoris* from the eastern Pacific.

Numerous recent publications have dealt with the taxonomy and systematics of certain genera within the Discodorididae Bergh, 1891. These publications all agree that the systematic placement of the genera *Hoplodoris* and *Carminodoris* is problematic. The difficulty begins to a large degree with the description of each genus. For example, Bergh's original descriptions (1880, 1889 respectively) did not include details of the external morphology or coloration found on the living animals. The descriptions also did not include details of the reproductive system, particularly in the case of *Carminodoris*. For instance, there is no illustration of the female reproductive organs for this genus. Diagnostic details are also missing for *Hoplodoris*, such as the ampulla that is not illustrated.

The absence of additional specimens for comparison from either type locality or from other geographic areas has added to diagnostic difficulties. For both genera, the type species have neither been collected nor described in detail since the 1880s.

The present study has been undertaken for three reasons. First, several specimens of Discodorididae from or near the type localities of the type species of *Carminodoris* (Mauritius) and *Hoplodoris* (Palau) are in the collections of the California Academy of Sciences (designated as

CASIZ) and the Australian Museum, Sydney (designated as C). Upon examination of these specimens, it became apparent that they conform largely to the original descriptions presented by Bergh 1889, with further key anatomical details becoming obvious using more powerful microscopy. These specimens are described here and illustrated. Also, examination of recently collected specimens of *Hoplodoris* revealed two new species whose combination of morphological characters differ markedly from previously described species. These two new species are described herein.

The second reason for this study is that modern phylogenetic techniques have not been previously used to separate closely related taxa within the Discodorididae. Valdés presented the first phylogeny that included all Discodorididae although in his study, he did not include all species of each genus. In the present study, we use morphological characters derived from all described species of *Hoplodoris* and *Carminodoris* and apply the criterion of maximum parsimony to determine their systematic placement.

Finally, Valdés' recent publication (2002) of the systematics of the Cryptobranchia allows us to compare morphological characters of *Hoplodoris* and *Carminodoris* to determine which are plesiomorphic, due to common ancestry, and which may be the result of independent acquisition. In his publication, Valdés (2002) also provides further description of two additional type species of Discodorididae *Discodoris boholiensis* Bergh, 1877 and *Geitodoris planata*, that we were able to use in our analysis.

SPECIES DESCRIPTIONS

Family Discodorididae Bergh, 1891

Genus *Hoplodoris* Bergh, 1880

Type species *Hoplodoris desmoparypha* Bergh, 1880, by monotypy. = *Carminodoris* Bergh, 1889.

Type species *Carminodoris mauritiana* Bergh, 1891, by monotypy.

Hoplodoris grandiflora (Pease, 1860)

Figs. 1–16

= *Doris grandiflora* Pease, 1860:30–31.

= *Doris grandifloriger* Abraham, 1877:206.

= *Hoplodoris desmoparypha* Bergh, 1880:51–56, pls. A–F.

= *Carminodoris mauritiana* Bergh, 1891:818–821, pl. 80, fig. 27, pl. 81, figs. 1–12.

= *Dendrodoris grandiflora* (Pease, 1860) in Pruvot-Fol, 1947:108.

Carminodoris grandiflora (Pease, 1860) in Kay & Young, 1969:185–186, fig. 12

= *Hoplodoris* sp. in Ono, 1999:114, fig. 186.

REMARKS ON SYNONYMY.—The name *Doris grandiflora* Pease, 1860 is a primary junior homonym of *Doris grandiflora* Rapp. Rapp's species is now placed in *Dendrodoris* and Pease's species is placed in *Hoplodoris*. Since these species have been considered as being in different genera after 1899, Article 23.9.5 of the International Code of Zoological Nomenclature states that these junior homonyms should not automatically be replaced. Both names have been in common usage and suppressing either would be disruptive, thus both names should be retained.

MATERIAL EXAMINED.—CASIZ 070388, one specimen, dissected, 44 mm, Saint Gilles les Bains, Reunion. Collected by T.M. Gosliner, 20 April 1989; CASIZ 073243, two specimens, dissected, 18 & 23 mm, Ile Saint Marie, Madagascar. Collected by H. Chaney, 5 April 1990; CASIZ 099336, one specimen, dissected, 30 mm, Mtwara Region, Tanzania. Collected by T.M. Gosliner, 4 November 1994; CASIZ 071866, one specimen, dissected, 44 mm, Sumilon Island, Philippines. Collected by G. Cornfield, 11 November 1987; CASIZ 109746, six specimens, two dissected, Island Reef, Ngermutideck, Palau. Collected by L. Sharon, 20 September 1996; CASIZ 068657,

one specimen, 17 mm, Daphne's Reef, between Wongat and Sinub Islands, Madang, Papua New Guinea. Collected by T.M. Gosliner, 15 August, 1989; CASIZ 075106, one specimen, dissected, 54 mm, Kaneohe Bay, Oahu, Hawaii. Collected by T.M. Gosliner, 1 March 1991; CASIZ 075164, one specimen, 30 mm, Hawaii. Collected by T.M. Gosliner, 1 December 1991; CASIZ 093684, one specimen, 4 mm, Hekili Point, Maui, Hawaii. Collected by C. Pittman, 1 October 1993; CASIZ 089650, one specimen, 16 mm, Hekili Point, Maui, Hawaii. Collected by C. Pittman, 26 September 1993; CASIZ 117374, one specimen, dissected, 48 mm, Hawaii Kai Marina, Oahu, Hawaii. Collected by D. Takaoka, 17 February 1999; CASIZ 106475, one specimen, dissected, 25 mm, Moalboal area, Cebu Island, Philippines. Collected by T.M. Gosliner, 24 April 1996; CASIZ 106563, one specimen, 13 mm, Kasai Beach, Moalboal area, Cebu Island, Philippines. Collected by T.M. Gosliner, 25 April 1996; CASIZ 106435, one specimen, 10 mm, Kasai Beach, Moalboal area, Cebu Island, Philippines. Collected by T.M. Gosliner, 25 April 1996.

DISTRIBUTION.— This species is known from Hawaii (present study), from the Philippines (present study), Tanzania (present study), Palau (present study), Mauritius (Bergh 1891), Kerama Island and from Madagascar (present study).

EXTERNAL MORPHOLOGY (Fig. 1).— The preserved animals range from 23–55 mm in length. The body is oval, flat and the notum is covered with large, rounded tubercles that decrease in size towards the mantle edge. The rhinophores are closely-set and stout, with a knob-shaped lamellar region (10–15 lamellae) that terminates in a point. The low rhinophore sheaths have an irregular edge and small tubercles on the sides. The six main gill leaves are tripinnate, feathery and the tubercle-covered sheath has a scalloped edge.

The ground color of the notum is light to medium mottled brown or tan. Lateral to either side of the dorsal median on some specimens are evenly spaced clumps of darker tubercles (Fig. 1E). Some specimens have dark spots near the mantle edge (Fig. 1F) or have areas of white tubercles that appear as perpendicular rays along the mantle edge (Fig. 1D). The clumps of dark tubercles merge on some specimens into a dark ring (Fig. 1B). On the knobby tops of some tubercles, the brown coloration appears worn off and whitish coloration is visible (Fig. 1A). The gill leaves are lighter tan than the body color, with a frosted appearance on the tips. The rhinophores are also lighter tan than the body and the tips are white.

On the ventral side of some preserved specimens, dark spots are sprinkled randomly. The digitate oral tentacles have also retained some of the dark speckles, and the oral tube has dark coloration. The foot is notched at the anterior end.

BUCCAL ARMATURE.— The buccal mass is large and muscular. At the anterior end of the muscular region is a thin, chitinous labial cuticle. The labial cuticle contains irregularly tipped jaw rodlets (Figs. 2A–B, 3A–B, 4A, 7A, 8A–B). The radular formulae of the specimens dissected are $30 \times 70.0.70$ $30 \times 116.0.116$ (CASIZ 070388), $33 \times 60.0.60$ (CASIZ 073243, specimen 1), $27 \times 40.0.40$ (CASIZ 073243, specimen 2), $30 \times 60.0.60$ (CASIZ 099336), $32 \times 75.0.75$ (CASIZ 071866), $30 \times 70.0.70$ (CASIZ 075106) and $26 \times 41.0.41$ (CASIZ 106475). The innermost lateral teeth are hamate, with no denticles visible on either edge (Figs. 3C, 4B), but some specimens have 6–7 minute denticles visible on the inner and outer edges (Figs. 5A, 8C). The middle radular teeth have a more elongate cusp, with small denticles (Figs. 2C–F) with up to 14 minute denticles (Figs. 5B–D) on the outer edge. The outer lateral teeth have small denticles (Figs. 2F, 3F, 4D, 5C, 7E) and the two or three penultimate lateral teeth are much shorter than the others, and are hamate (Figs. 2F, 3F, 4F, 5C, 6C, 7D–E, 8F).

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Figs. 9A, 12, 15). The ampulla is thick and tubular and lies tightly between the female gland mass and prostate gland. The ampulla narrows slightly into the postampullary duct, which bifurcates into the oviduct and vas

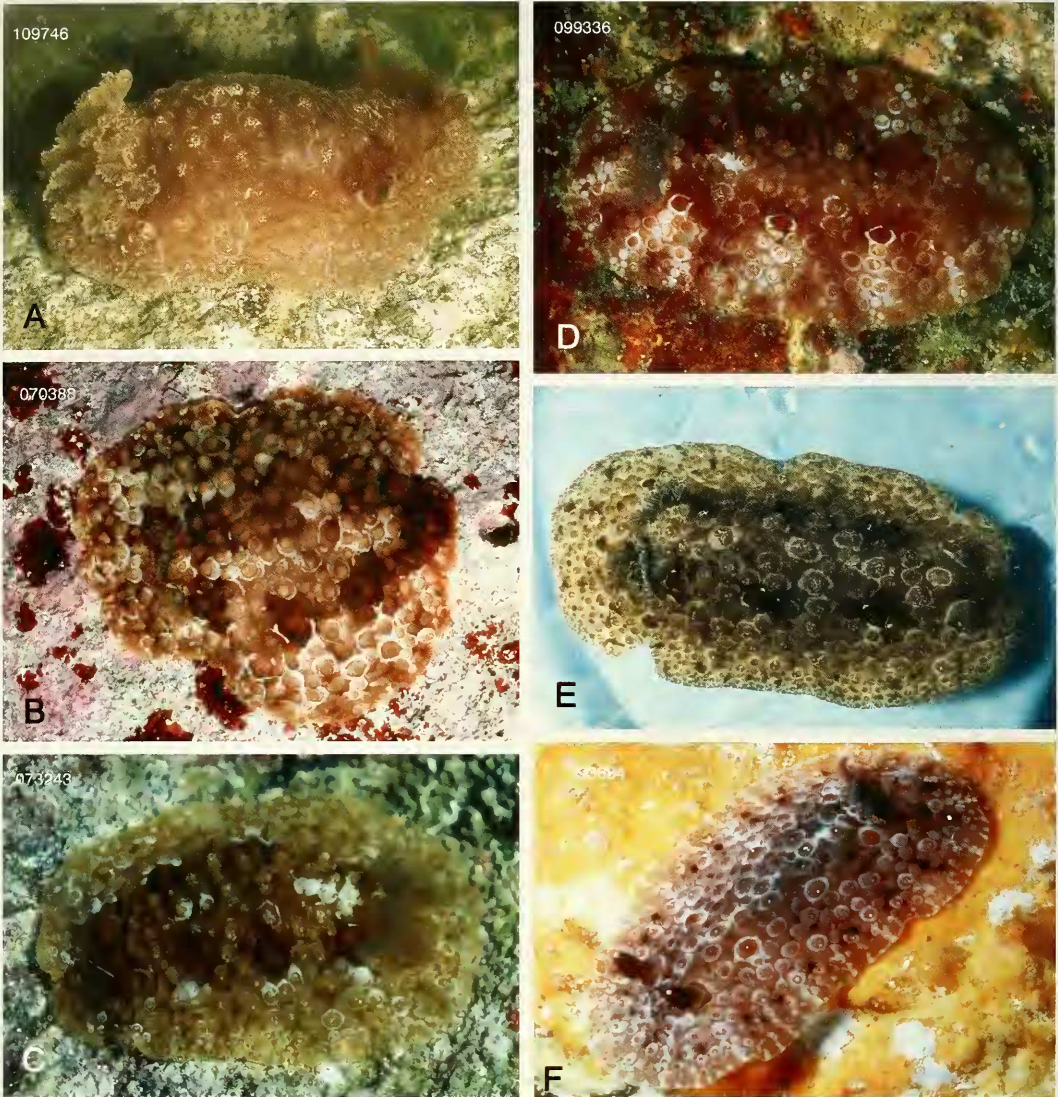


FIGURE 1. *Hoplodoris grandiflora*. Living animals. – A. Palau (CASIZ 109746) 40 mm. Photo taken by T.M. Gosliner. – B. Reunion (CASIZ 070388) 44 mm. Photo taken by T.M. Gosliner. – C. Madagascar (CASIZ 073243) 23 mm. Photo taken by T.M. Gosliner. – D. Tanzania (CASIZ 099336) 30 mm. Photo taken by T.M. Gosliner. – E. Hawaii (CASIZ 075106) 54 mm. Photo taken by T.M. Gosliner. – F. Hawaii (CASIZ 093684) 4 mm. Photo taken by P. Fiene.

deferens. The short oviduct enters the female gland mass. The prostate is a large mass which narrows into the long, highly convoluted, deferent duct. The prostate has two distinct glandular types that are differentially pigmented. The deferent duct then widens into the penial bulb, which lies next to the vagina. The penis is armed on the inside with short, pointed thorn-like structures (Figs. 10A–D, 13A–B, 16A–B).

The short uterine duct emerges from the female gland mass and joins the receptaculum seminis at the duct that connects the receptaculum seminis to the bursa copulatrix. This duct is moderately short. The pyriform receptaculum seminis is nearly one-third the size of the bursa copulatrix.

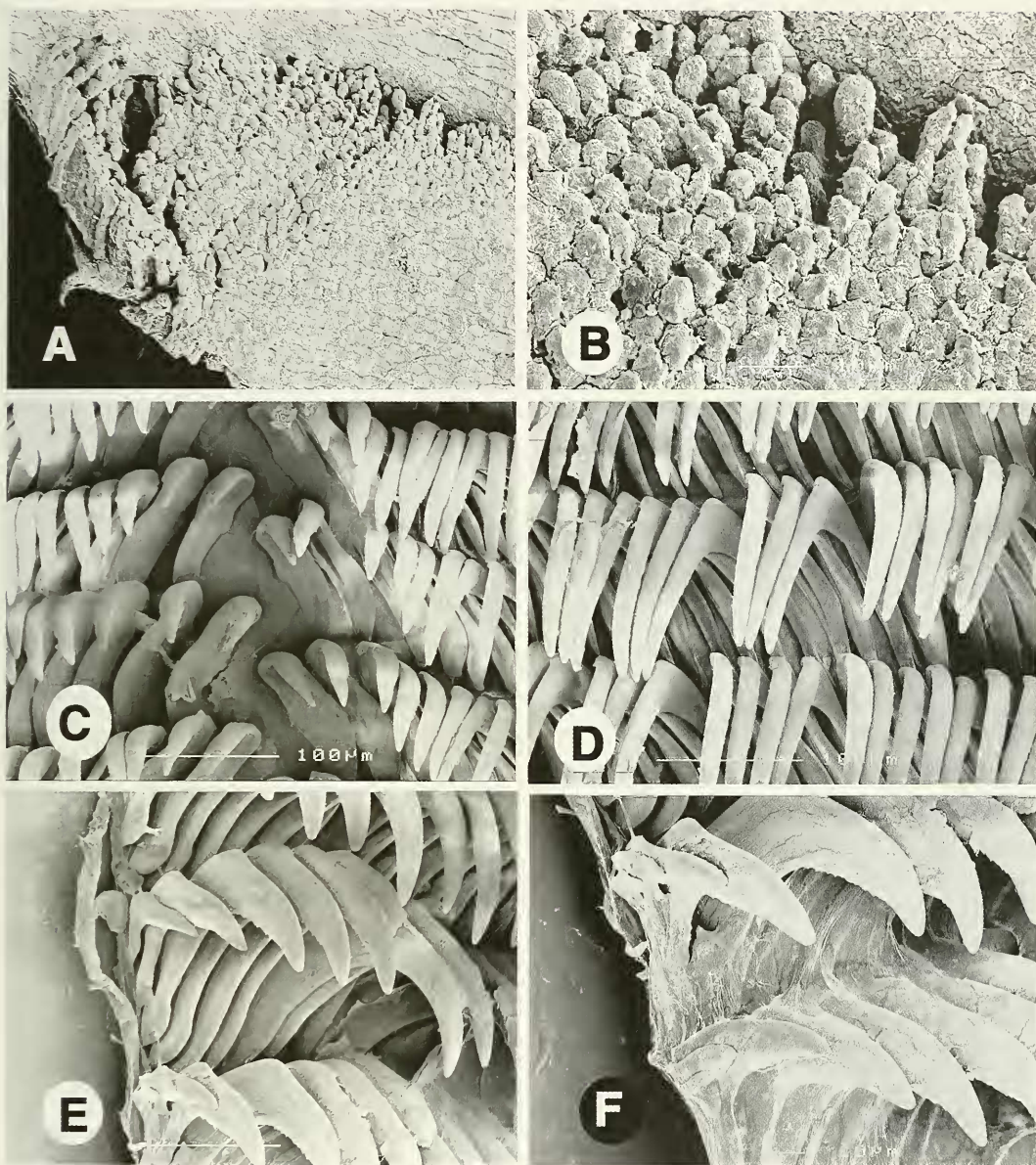


FIGURE 2. *Hoplodoris grandiflora* Palau (CASIZ 109746) radula. – A. Labial rods. Scale bar = 1 μ m. – B. Labial rods, close-up. Scale bar = 10 μ m. – C. Inner lateral teeth. Scale bar = 100 μ m. – D. Middle lateral teeth. Scale bar = 100 μ m. – E. Outer lateral teeth. Scale bar = 10 μ m. – F. Outer lateral teeth, close-up. Scale bar = 10 μ m.

The bursa is partially enveloped by the prostate. The moderately long, thin, convoluted vaginal duct emerges from the base of the bursa then widens into the vagina. The vagina is also armed with small hooks (Figs. 11, 13C, 16C–D).

At the genital atrium, is a long, tubular, blind-ended vestibular gland. This gland has a convoluted, narrow region just prior to a bulb-like terminus at the opening into the genital atrium. Inside the bulb-like terminus is a hollow stylet (Figs. 10F, 13D, 14, 16E–F).

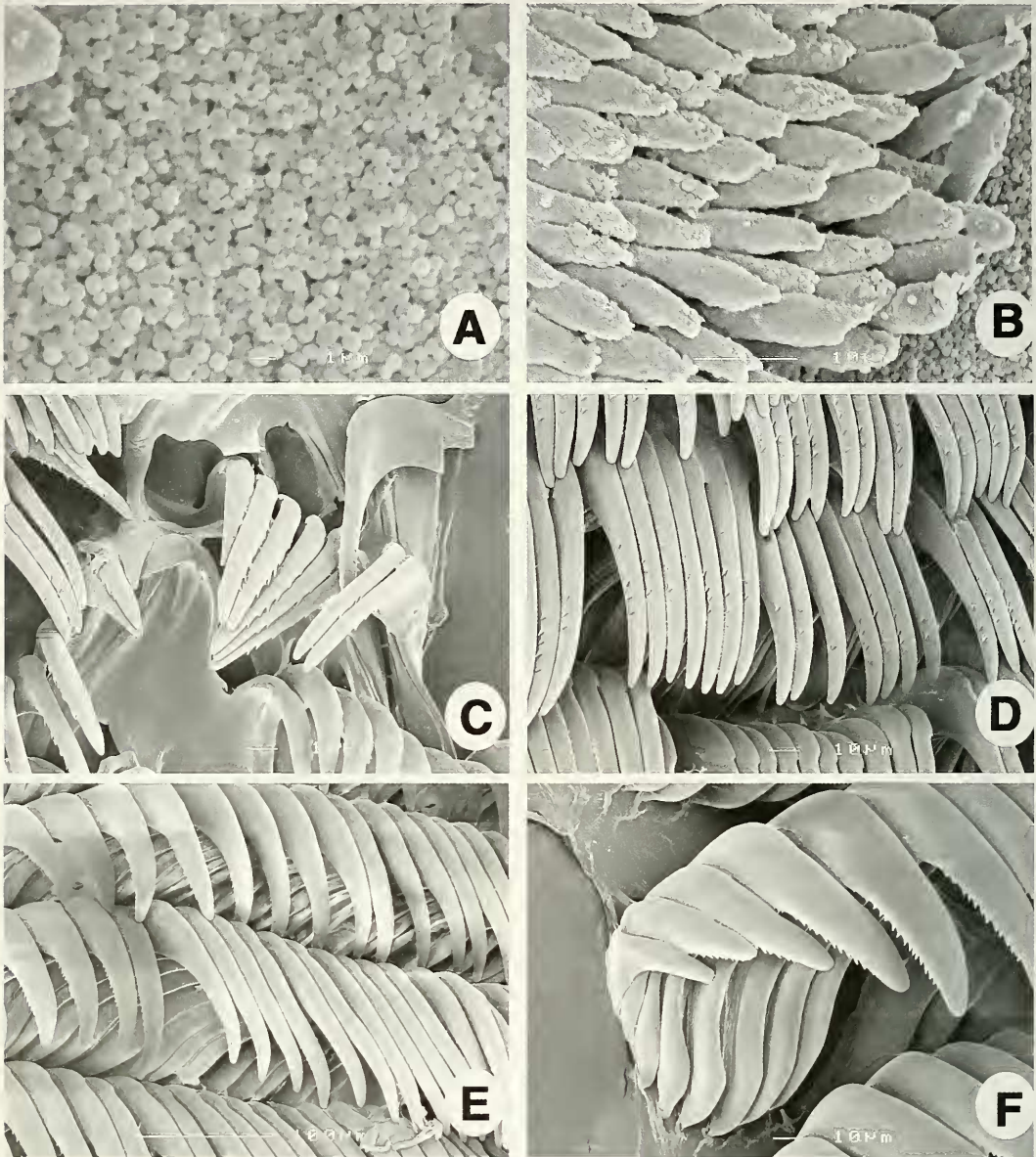


FIGURE 3. *Hoplodoris grandiflora* Reunion (CASIZ 070388) radula. Scale bar = 1 μm. – A. Labial rods. Scale bar = 1 μm. – B. Labial rods, close-up. Scale bar = 10 μm. – C. Inner lateral teeth. Scale bar = 10 μm. – D. Middle lateral teeth. Scale bar = 10 μm. – E. Middle lateral teeth. Scale bar = 100 μm. – F. Outer lateral teeth. Scale bar = 10 μm.

REMARKS.— Since Bergh's (1880) original description of *Hoplodoris*, several authors have recently described the characters that unite the genus. Thompson (1975), Miller (1991), and Valdés (2002) each provided an elaboration of Bergh's 1880 diagnostic of the genus *Hoplodoris*. Gosliner and Behrens (1998) and Miller (1991) provided further details on the anatomy of the type species *Hoplodoris desmoparypha*. Burn (1969) also used some of the generic diagnostics to place *Doris nodulosa* within the genus *Hoplodoris*.

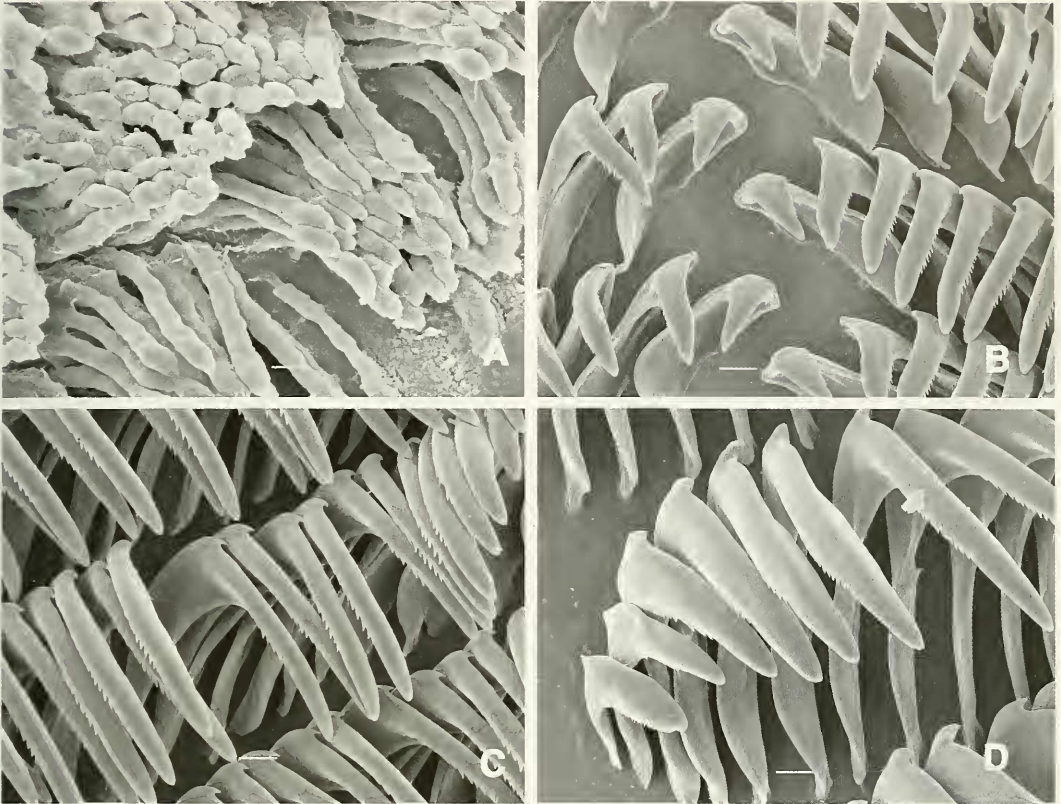


FIGURE 4. *Hoplodoris grandiflora* Philippines (CASIZ 071866) radula. – A. Labial rods. Scale bar = 10 μ m. – B. Inner lateral teeth. Scale bar = 100 μ m. – C. Middle lateral teeth. Scale bar = 100 μ m. – D. Outer lateral teeth. Scale bar = 10 μ m.

The same authors also discussed the similarities between *Hoplodoris* and the genus *Carminodoris*. In addition to these authors, Kay and Young (1969) briefly mentioned some characters of *Carminodoris* in their account of two species from Hawaii (*C. grandiflora* and *C. nodulosa*).

The difficulty in distinguishing these two genera has been primarily due to the deficiencies of the original descriptions and the absence of additional specimens of the type species since the 1880's. However, the examination of discodoridid specimens housed at the California Academy of Sciences and the Australian Museum, Sydney, that were collected from or near the type localities of *Hoplodoris* and *Carminodoris* provided further anatomical information on both genera. Recent collections of *Hoplodoris* specimens from Bali and Costa Rica also provided further insight to the varied morphology of this genus.

From our examination we are certain that our specimens from Palau do in fact represent the animals Bergh described in 1880 as *Hoplodoris desmoparypha*. They match almost all features included by Bergh in the original description. There are two primary differences we noted with our specimen. One is that some of the outer lateral teeth have very minute denticles on their outer edge, that are nearly impossible to see even with a modern compound microscope. We observed them only by high power scanning electron microscopy (SEM). The second difference is the presence of an armed vagina in our material. This feature could easily have been missed by Bergh (1880).

Our specimens from Madagascar and Tanzania match all features of Bergh's (1889) original

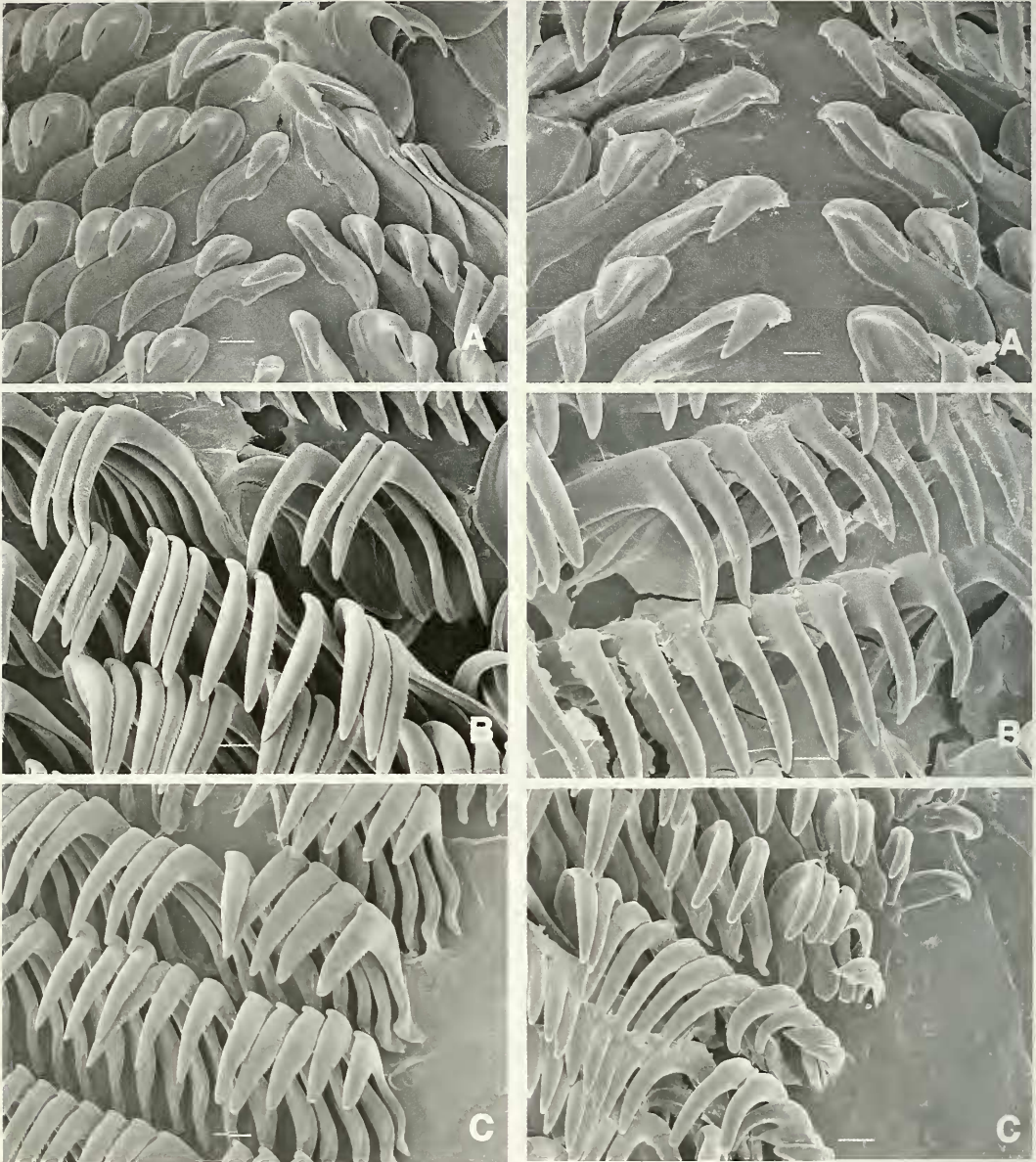


FIGURE 5 (Left). *Hoplodoris grandiflora* Madagascar (CASIZ 073243) radula. – A. Inner lateral teeth. Scale bar = 10 μ m. – B. Middle lateral teeth. Scale bar = 100 μ m. – C. Outer lateral teeth. Scale bar = 10 μ m.

FIGURE 6 (Right). *Hoplodoris grandiflora* Philippines (CASIZ 106475) radula. – A. Inner lateral teeth. Scale bar = 100 μ m. – B. Middle lateral teeth. Scale bar = 100 μ m. – C. Outer lateral teeth. Scale bar = 10 μ m.

description of *Carminodoris mauritiana*. Although the only drawing of the reproductive organs that Bergh provided was of the armed penis, we observed a vestibular gland that contains a spine. In Bergh's (1889) description of *C. mauritiana*, he mentioned a special gland that seemed to open near the mucus gland at the genital opening. It is likely that this "special gland" is the vestibular gland that we found in our specimens. We also observed an armed vagina that Bergh could have over-

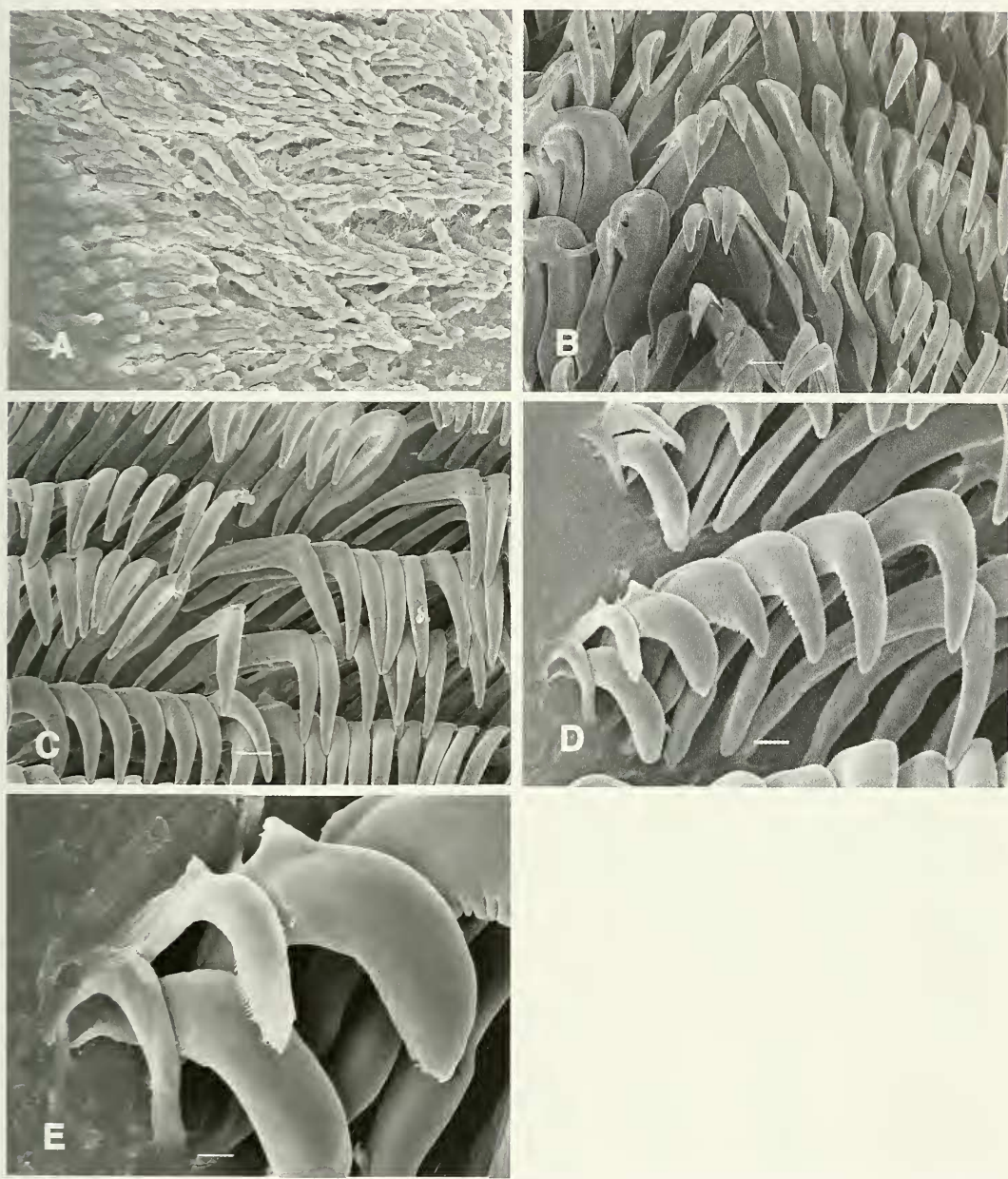


FIGURE 7. *Hoplodoris grandiflora* Hawaii (CASIZ 117374) radula. – A. Labial rods. Scale bar = 1 μ m. – B. Inner lateral teeth. Scale bar = 10 μ m. – C. Middle lateral teeth. Scale bar = 100 μ m. – D. Outer lateral teeth. Scale bar = 10 μ m. – E. Outer lateral teeth, close-up. Scale bar = 1 μ m.

looked in his examination. With the addition of these probably overlooked characters, Bergh's descriptions of *Hoplodoris desmoparypha* and *Carminodoris mauritiana* are nearly identical.

In addition, the specimen we examined from Hawaii (the type locality of *Carminodoris grandiflora*) matches the description of this species by Pease and Kay and Young. These descriptions match those of Bergh's for *C. mauritiana* in all respects, when taking into consideration the armed

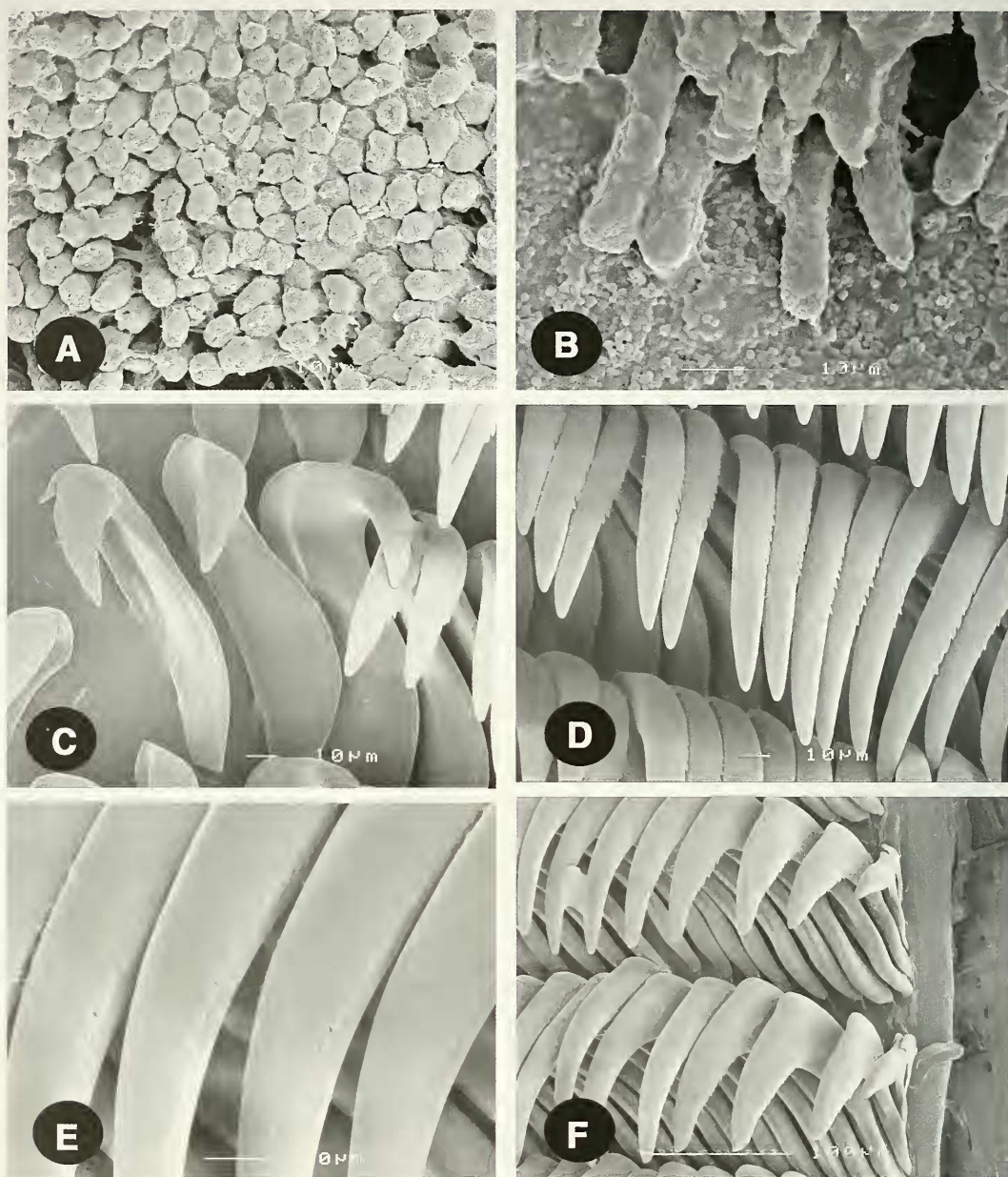


FIGURE 8. *Hoplodoris grandiflora* Hawaii (CASIZ 075106) radula. – A. Labial rods. Scale bar = 10 μ m. – B. Labial rods, close-up. Scale bar = 10 μ m. – C. Inner lateral teeth. Scale bar = 10 μ m. – D. Middle lateral teeth. Scale bar = 10 μ m. – E. Middle lateral teeth, close-up. Scale bar = 10 μ m. – F. Outer lateral teeth. Scale bar = 100 μ m.

vagina. All three species, *Hoplodoris desmoparypha*, *C. mauritiana* and *C. grandiflora* appear to be the same, with the variations that we found due to our more advanced microscopic techniques. The phylogenetic analyses performed during this study also confirm that these three species remain a trichotomy when using maximum parsimony as an optimality criterion (see the following phylogenetic analysis).

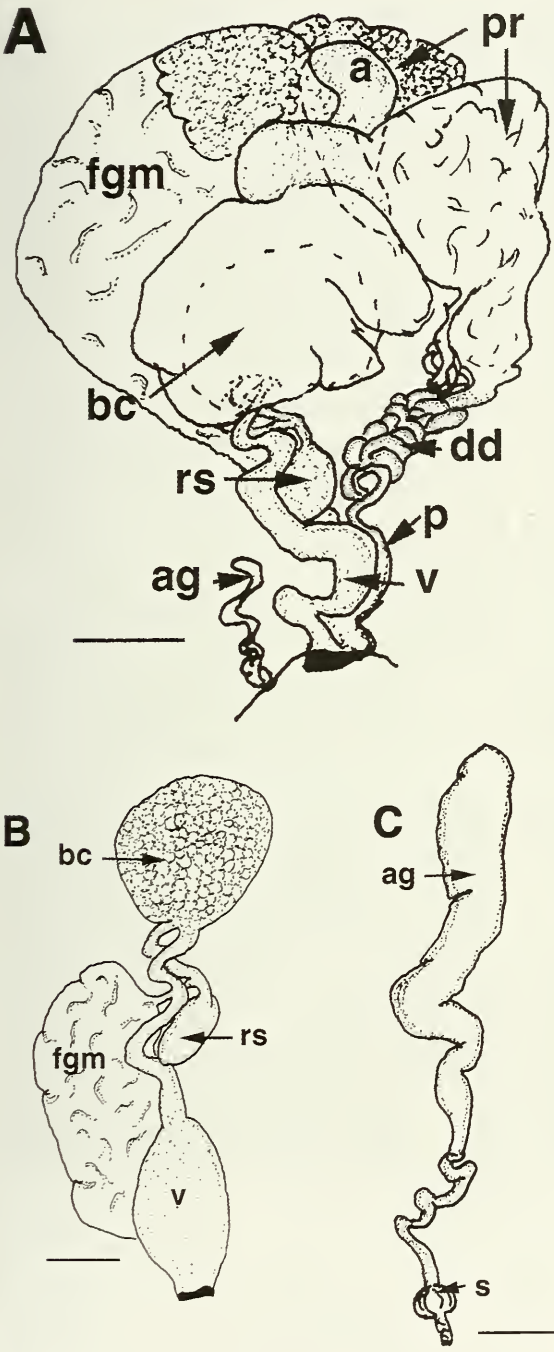


FIGURE 9. *Hoplodoris grandiflora* Palau (CASIZ 109746) reproductive system. – A. Schematic drawing of entire reproductive system. Scale bar = 1 mm. – B. Schematic expansion of female reproductive organs. Scale bar = 0.5 mm. – C. Schematic expansion of accessory gland. Scale bar = 0.14 mm. Abbreviations: a, ampulla; ag, accessory gland; bc, bursa copulatrix; dd, deferent duct; fg, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; s, stylet (accessory gland); v, vagina.

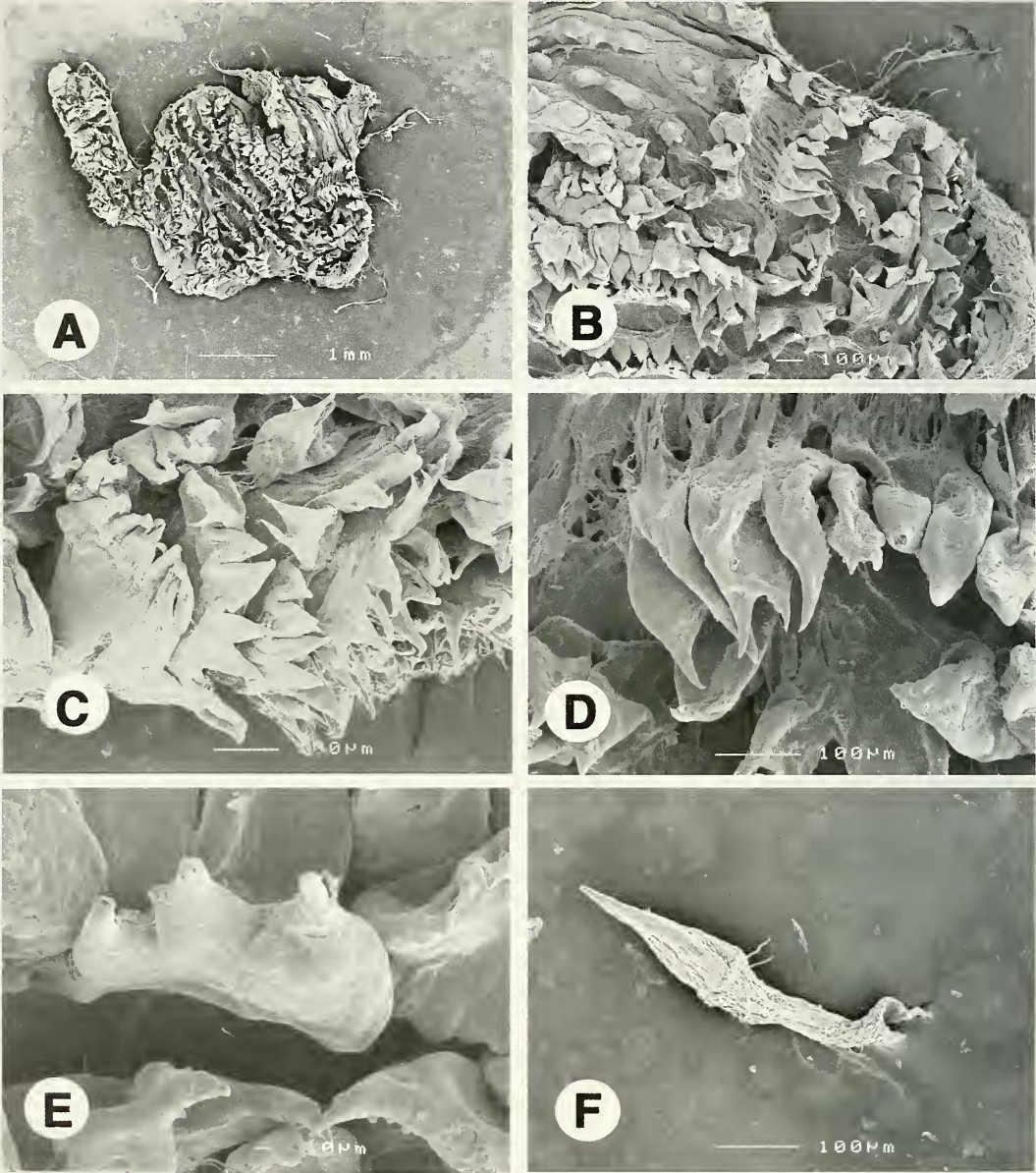


FIGURE 10. *Hoplodoris grandiflora* Palau (CASIZ 109746) detail of genital armament. – A. Entire penis dissected and opened to show armament. Scale bar = 1 mm. – B. Close-up detail of rows of spines. Scale bar = 100 µm. – C. Close-up detail of spines. Scale bar = 100 µm. – D. Close-up detail of spines. Scale bar = 100 µm. – E. Close-up detail of different form of spine. Scale bar = 10 µm. – F. Close-up detail of accessory gland stylet. Scale bar = 100 µm.

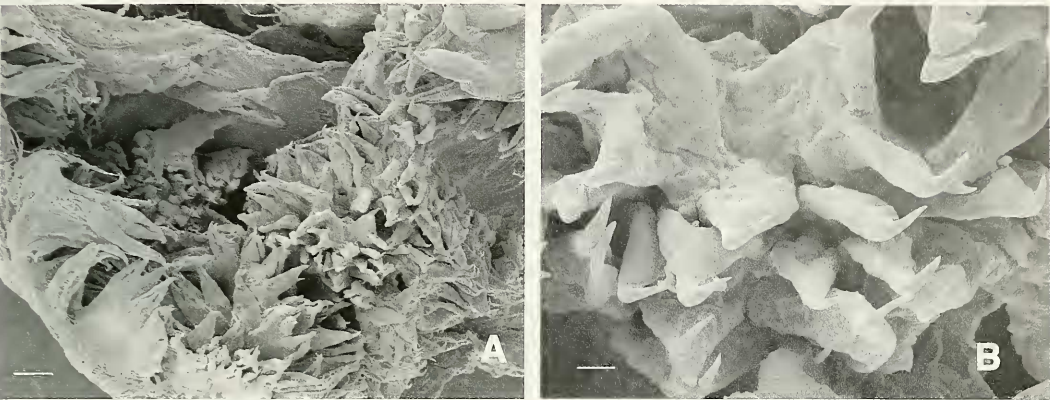


FIGURE 11. *Hoplodoris grandiflora* Palau (CASIZ 109746) detail of genital armament. –A. Vagina dissected and opened to show armament. Scale bar = 30 μ m. –B. Close-up detail of rows of spines. Scale bar = 100 μ m.

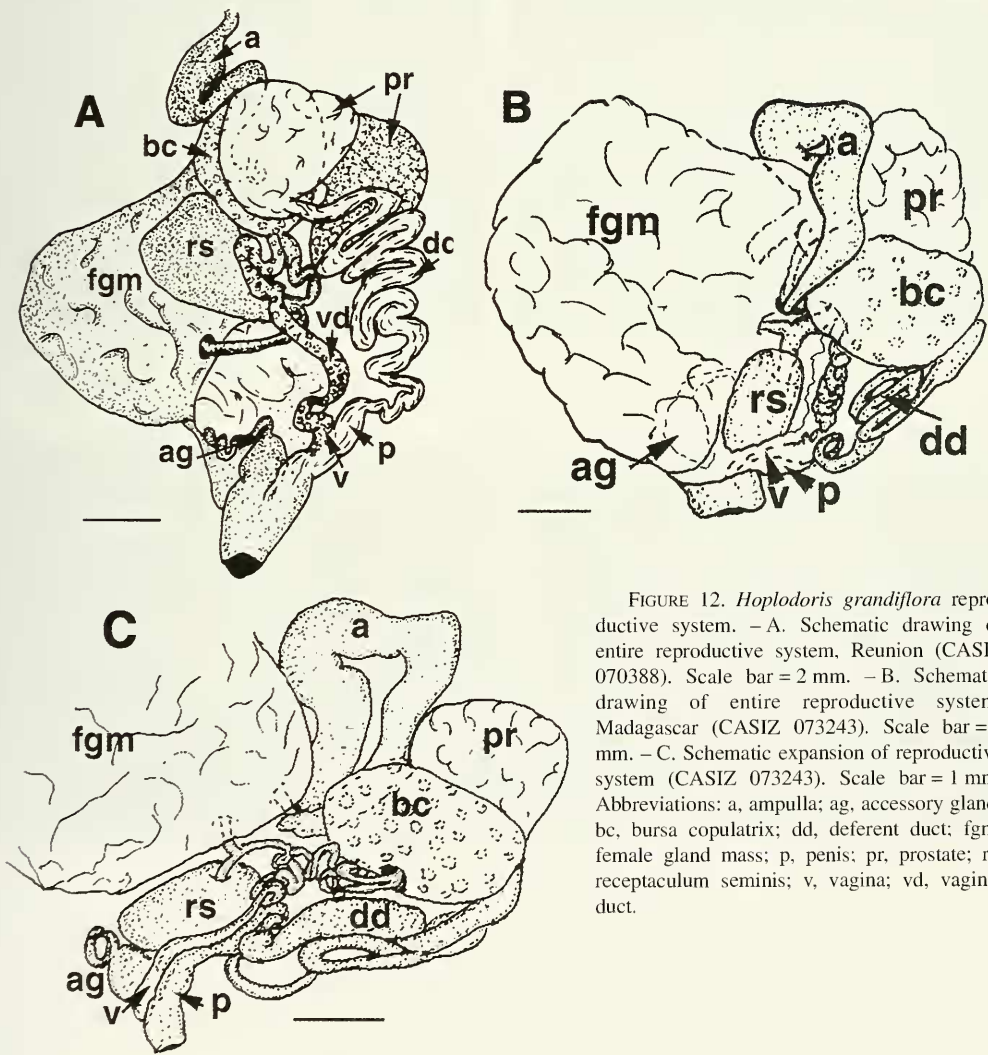


FIGURE 12. *Hoplodoris grandiflora* reproductive system. –A. Schematic drawing of entire reproductive system, Reunion (CASIZ 070388). Scale bar = 2 mm. –B. Schematic drawing of entire reproductive system, Madagascar (CASIZ 073243). Scale bar = 2 mm. –C. Schematic expansion of reproductive system (CASIZ 073243). Scale bar = 1 mm. Abbreviations: a, ampulla; ag, accessory gland; bc, bursa copulatrix; dd, deferent duct; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; v, vagina; vd, vaginal duct.

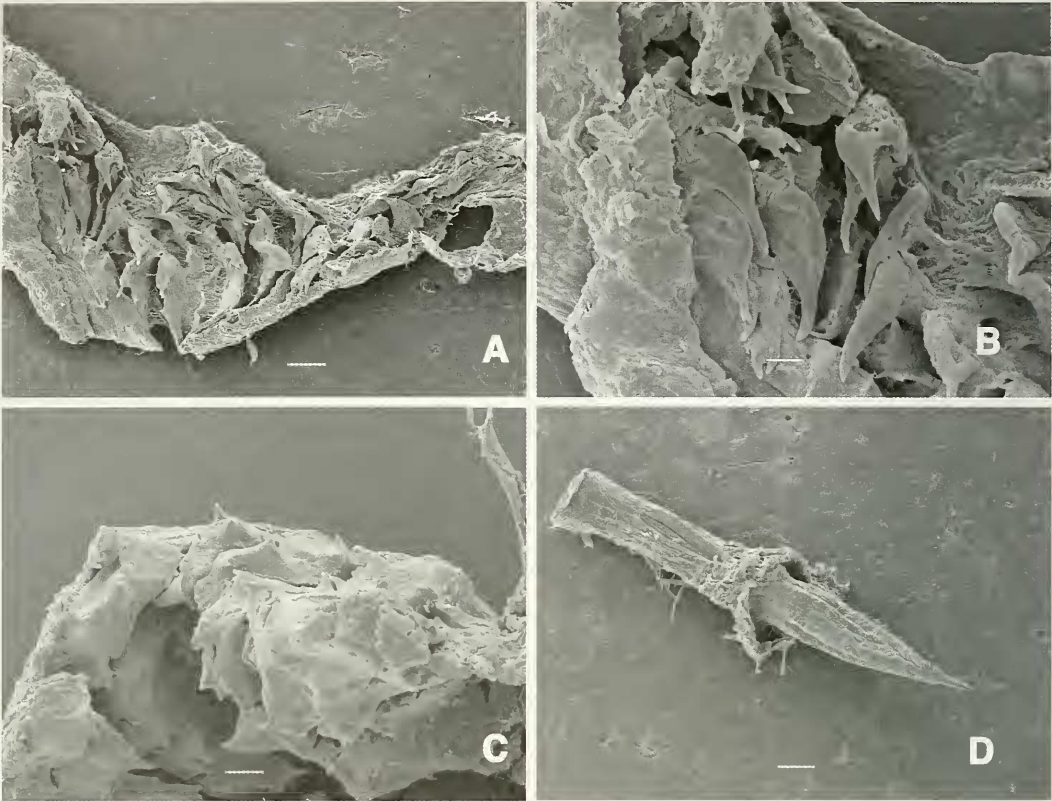


FIGURE 13. *Hoplodoris grandiflora* Madagascar (CASIZ 073243) genital armament. – A. Penis dissected and opened to show armament. Scale bar = 200 µm. – B. Close-up detail of rows of spines. Scale bar = 100 µm. – C. Vagina dissected and opened to show armament. Scale bar = 100 µm. – D. Close-up detail of accessory gland stylet. Scale bar = 100 µm.

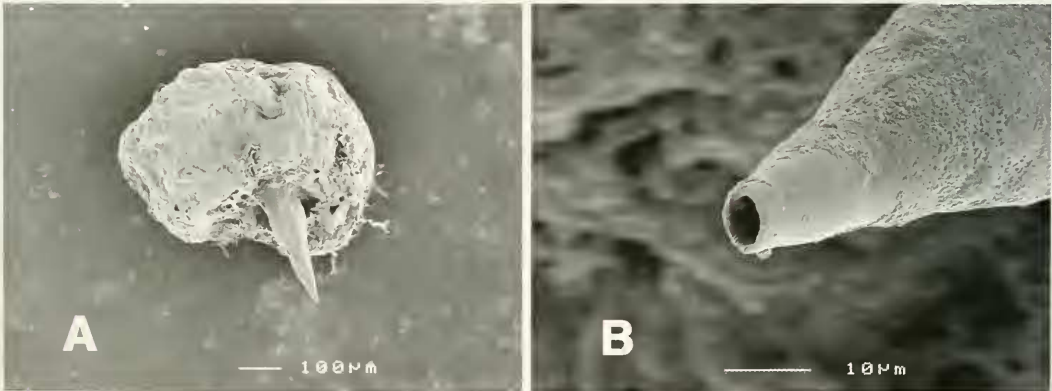


FIGURE 14. *Hoplodoris grandiflora* Reunion (CASIZ 070388) genital armature. – A. Dissected accessory gland stylet. Scale bar = 100 µm. – B. Close-up of hollow stylet. Scale bar = 10 µm.

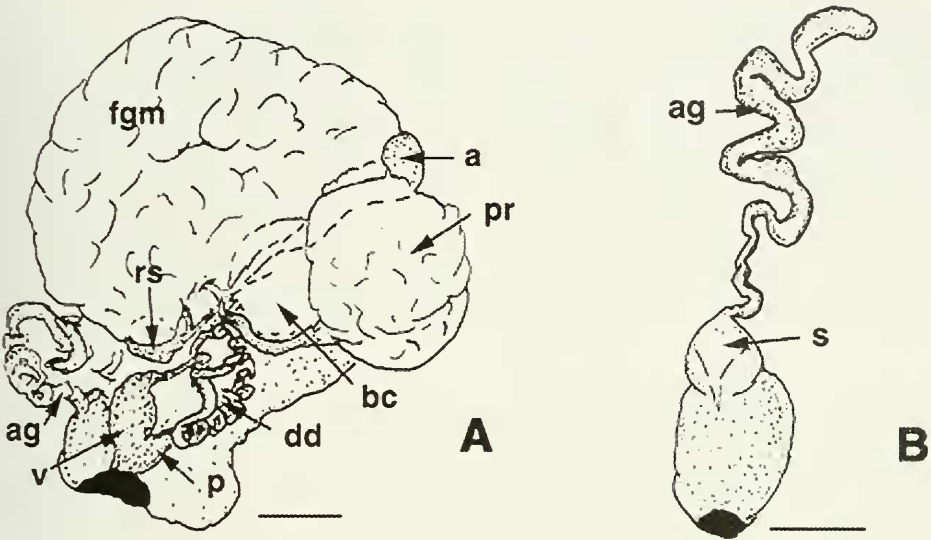


FIGURE 15. *Hoplodoris grandiflora* Hawaii (CASIZ 075106) reproductive system. – A. Schematic drawing of entire reproductive system. Scale bar = 2 mm. – B. Schematic expansion of accessory gland. Scale bar = 0.5 mm. Abbreviations: a, ampulla; ag, accessory gland; bc, bursa copulatrix; dd, deferent duct; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; s, stylet (accessory gland); v, vagina.

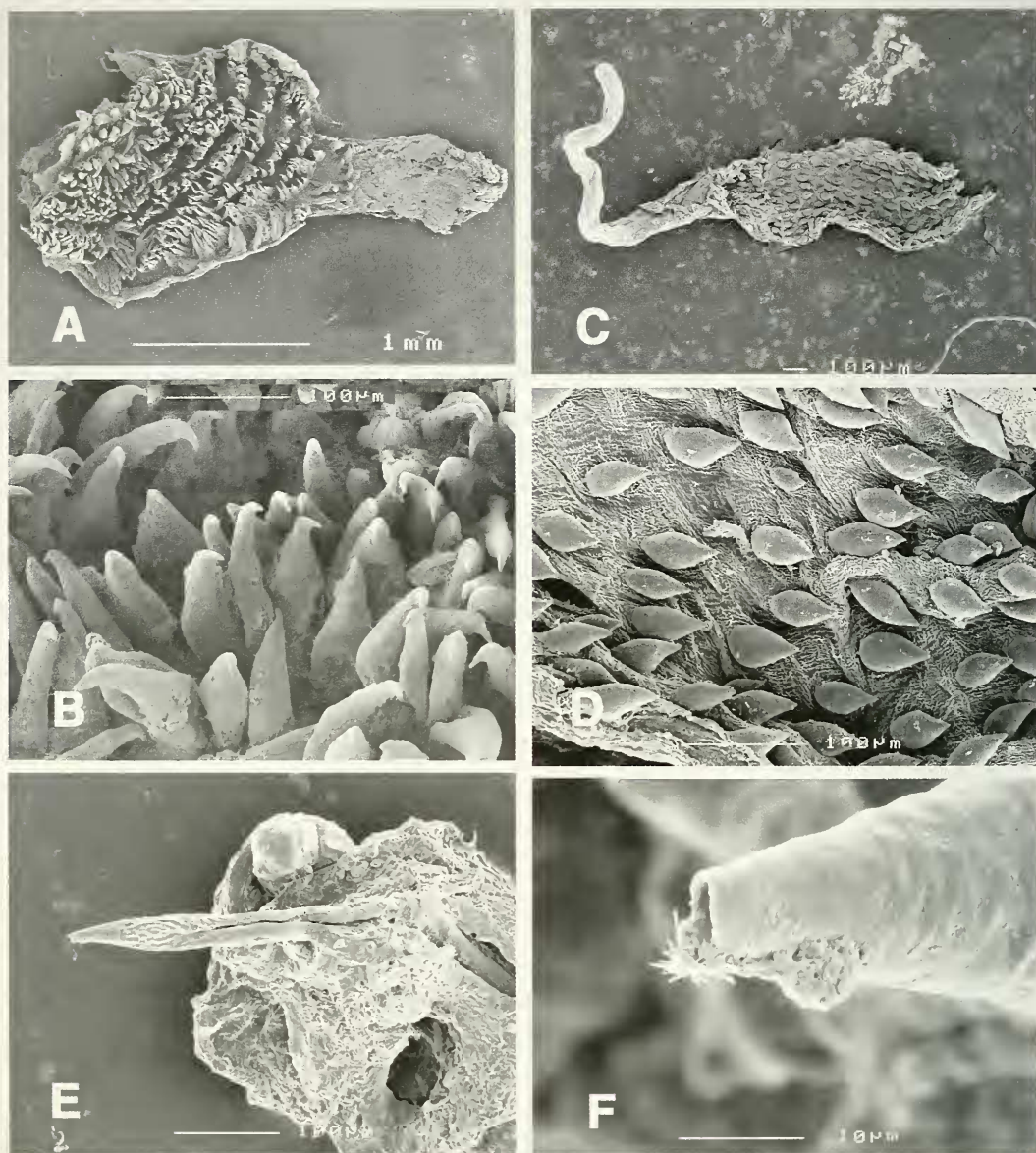


FIGURE 16. *Hoplodoris grandiflora* Hawaii (CASIZ 075106) genital armature. -A. Entire penis dissected and opened to show armament. Scale bar = 1 mm. -B. Close-up detail of rows of hooked spikes. Scale bar = 100 μ m. -C. Entire vagina dissected and opened to show armament. Scale bar = 100 μ m. -D. Close-up detail of vaginal spines. Scale bar = 100 μ m. -E. Accessory gland stylet. Scale bar = 100 μ m. -F. Close-up detail of accessory gland hollow stylet. Scale bar = 10 μ m.

Hoplodoris bifurcata (Baba, 1993)

Figs. 17A, B, 18–20

= *Carminodoris bifurcata* Baba, 1993:226–232, pls. 1, 7–10.= *Carminodoris nodulosa* (Angas, 1864) misidentification in Kay & Young, 1969:186–187, figs. 13, 18, Ala Moana, Oahu, Hawaii.= *H. nodulosa* (Angas, 1864) misidentification in Kay, 1979:462, fig. 148D, Oahu, Hawaii.= *Carminodoris bifurcata* Baba, 1993 in Keiu, S., 2000:98, fig. 143.= *H. nodulosa* (Angas, 1864) misidentification in Bertsch & Johnson, 1981:38, bottom fig., Hawaii.

MATERIAL EXAMINED.—CASIZ 070133, two specimens, one dissected, 30 mm, Seragaki Beach, Ryukyu Island, Okinawa. Collected by R.F. Bolland, 7 May 1989; CASIZ 087898, one specimen, dissected, 35 mm, dissected, Seragaki Beach, Ryukyu Island, Okinawa. Collected by R.F. Bolland, 21 August 1992; CASIZ 079197, one specimen, 31 mm, Seragaki Beach, Ryukyu Island, Okinawa. Collected by R.F. Bolland, 25 March 1991; CASIZ 079280, one specimen, 20 mm, Seragaki Beach, Ryukyu Island, Okinawa. Collected by R.F. Bolland, 7 September 1989; CASIZ 110428, two specimens, one dissected, 20 mm, Arthur's Place, Calumpan Peninsula, Batangas Province, Luzon, Philippines. Collected by T.M. Gosliner, 22 April 1997; CASIZ 106562, one specimen, 10 mm, Arthur's Place, Calumpan Peninsula, Batangas Province, Philippines. Collected by T.M. Gosliner, 17 April 1996; CASIZ 116736, one specimen, 28 mm, Blowhole, Oahu, Hawaii. Collected by S. Johnson, 23 February 1980; CASIZ 116650, one specimen, 10 mm, Pupukea, Oahu, Hawaii. Collected by S. Johnson, 8 July 1985; CASIZ 071561, one specimen, dissected, 32 mm, Sand Island, Kaneohe Bay, Oahu, Hawaii. Collected by T.M. Gosliner, 10 September 1987; CASIZ 097455, two specimens, 9, 16 mm, Napili Bay, Maui. Collected by T.M. Gosliner, 6 April 1994.

DISTRIBUTION.—This species is known from Hawaii (Kay and Young 1969; present study), Japan (Baba 1993), Philippines (present study) and from Okinawa (present study).

EXTERNAL MORPHOLOGY.—The living animals (Figs. 17A–B) range from 30–32 mm in length. The body is oval, flat and the notum is covered with large, round and tapered tubercles. The tubercles are mostly rounded on the dorsal median, becoming progressively more tapered around the median. The tubercles closest to the mantle edge are much smaller than the others. The coloration of the living animal is complex, and variegated. The ground color is light to medium gray, with mottled shades of darker grays and reddish-browns scattered over the mantle. There is a central dorsum, red-brown band of color, with all tubercles having the same coloration. On the tubercles towards the mantle edge, there is a white ring at the base followed by a red-brown or tan ring, and a white tip on some tubercles. Sprinkled randomly among the tubercles are tiny, dark brown or black spots. The long, tapered rhinophores have a light tan, short stalk with a darker tan, long lamellar portion (approximately 20 lamellae) that angles posteriorly and terminates with a white tip. The six posteriorly projecting gill leaves are tripinnate and feathery and the anterior leaves are light tan with whitish flecks of color, while the posterior leaves are red-brown. The rhinophore and gill sheaths are moderately tall and have tuberculate, irregular edges.

The ventral side of some preserved specimens has retained only a few randomly sprinkled dark spots. The long, pointed oral tentacles have not retained any color, and the foot is anteriorly notched.

BUCCAL ARMATURE (Fig. 18).—The buccal mass is large and muscular. At the anterior end of the muscular region is a thin, chitinous labial cuticle. The labial cuticle contains irregularly-tipped jaw rodlets (Figs. 18A–B). The radular formula of the specimen dissected is: 25×31.031 (CASIZ 070133). The innermost lateral tooth is hamate, bifid, with tiny finger-like projections on the inner

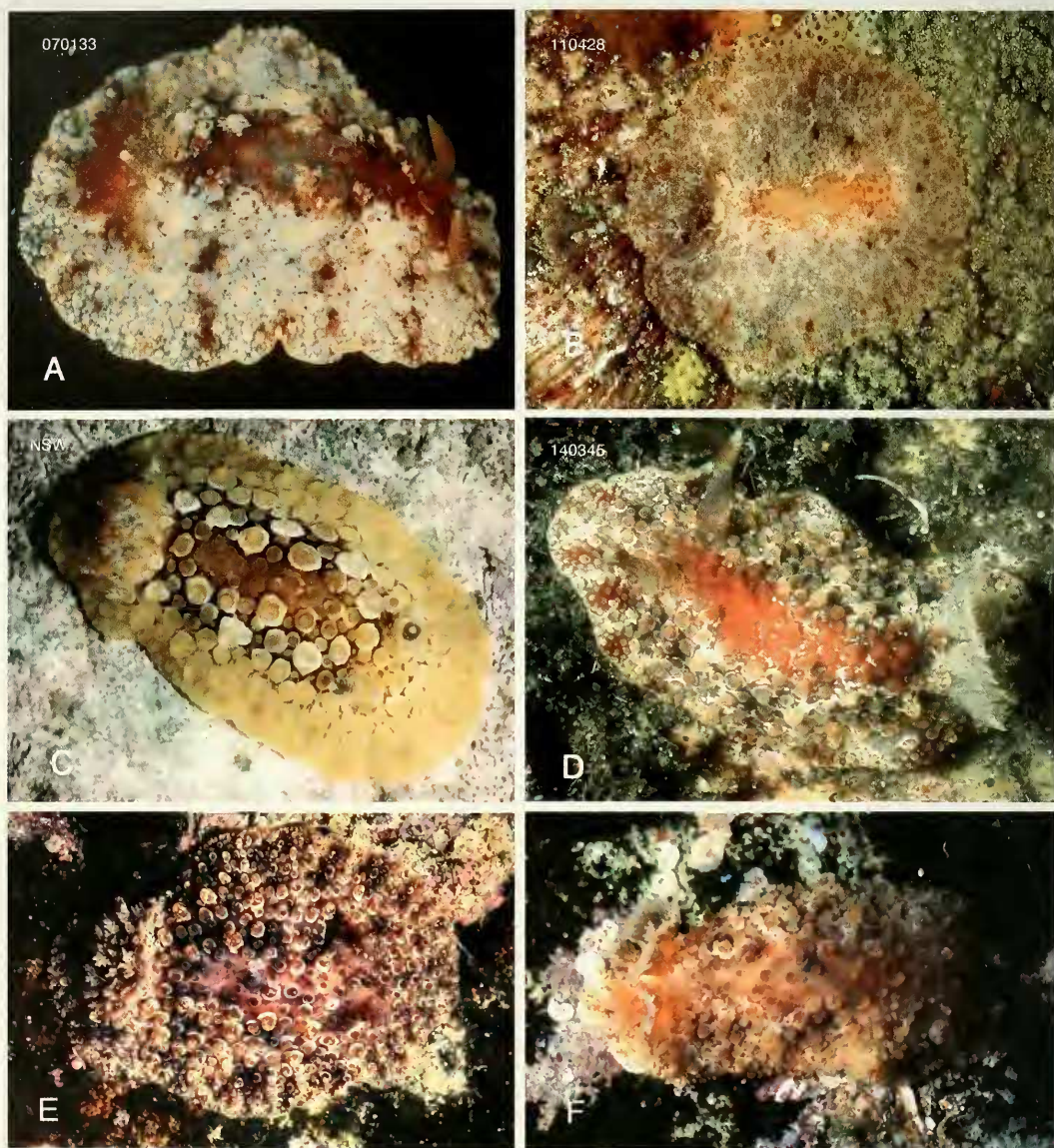


FIGURE 17. *Hoplodoris* spp. Living animals. — A. *Hoplodoris bifurcata*. (CASIZ 070133) (Okinawa) 32 mm. Photo taken by R.F. Bolland. — B. *Hoplodoris bifurcata* (CASIZ 110428) (Philippines) 20 mm. Photo taken by T.M. Gosliner. — C. *Hoplodoris nudulosa*. (New South Wales) (no length available). Photo taken by T.M. Gosliner. — D. *Hoplodoris flammea* (CASIZ 140345) (Bali) 24 mm. Photo taken by T.M. Gosliner. — E. *Hoplodoris bramale* (INB) (Costa Rica) 25 mm. Photo taken by T.M. Gosliner. — F. *Hoplodoris bramale* (INB) (Costa Rica) 18 mm. Photo taken by T.M. Gosliner.

edge and with about 5–8 minute denticles visible on the outer edge (Figs. 18C–D). The middle radular teeth have a more elongate cusp, also with 5–8 minute denticles (Fig. 18E). The two to three outermost lateral teeth are much shorter than the middle or inner teeth, are flat plates, and are denticulate (Fig. 18F).

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Figs. 19A–B). The ampulla is long, thin and tubular and lies between the female gland mass and prostate gland. The ampulla nar-

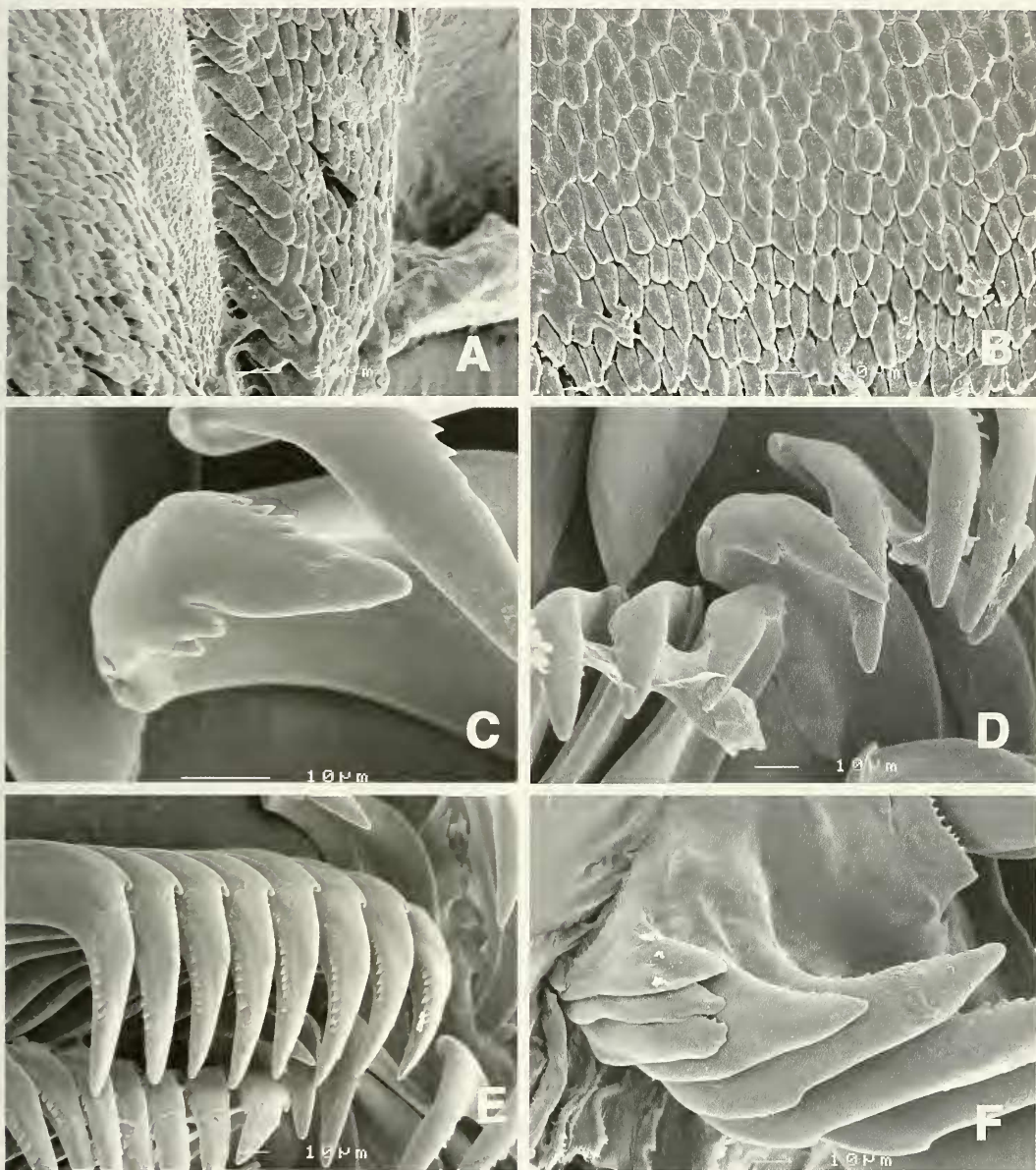


FIGURE 18. *Hoplodoris bifurcata* Okinawa (CASIZ 070133) radula. – A. Labial rods. Scale bar = 10 µm. – B. Labial rods, close-up. Scale bar = 10 µm. – C. Inner lateral teeth, close-up. Scale bar = 10 µm. – D. Inner lateral teeth. Scale bar = 10 µm. – E. Middle lateral teeth. Scale bar = 10 µm. – F. Outer lateral teeth. Scale bar = 10 µm.

rows slightly into the postampullary duct, which bifurcates into the oviduct and vas deferens. The short oviduct enters the female gland mass. The large prostate mass narrows into a long, looped deferent duct. The prostate has two distinct glandular types that are differentially pigmented. The deferent duct then widens into the penial bulb, which lies next to the longer, narrower vagina. The penis is sparsely armed on the inside with short, thorn-like structures (Fig. 20A).

The short uterine duct emerges from the female gland mass and joins the receptaculum sem-

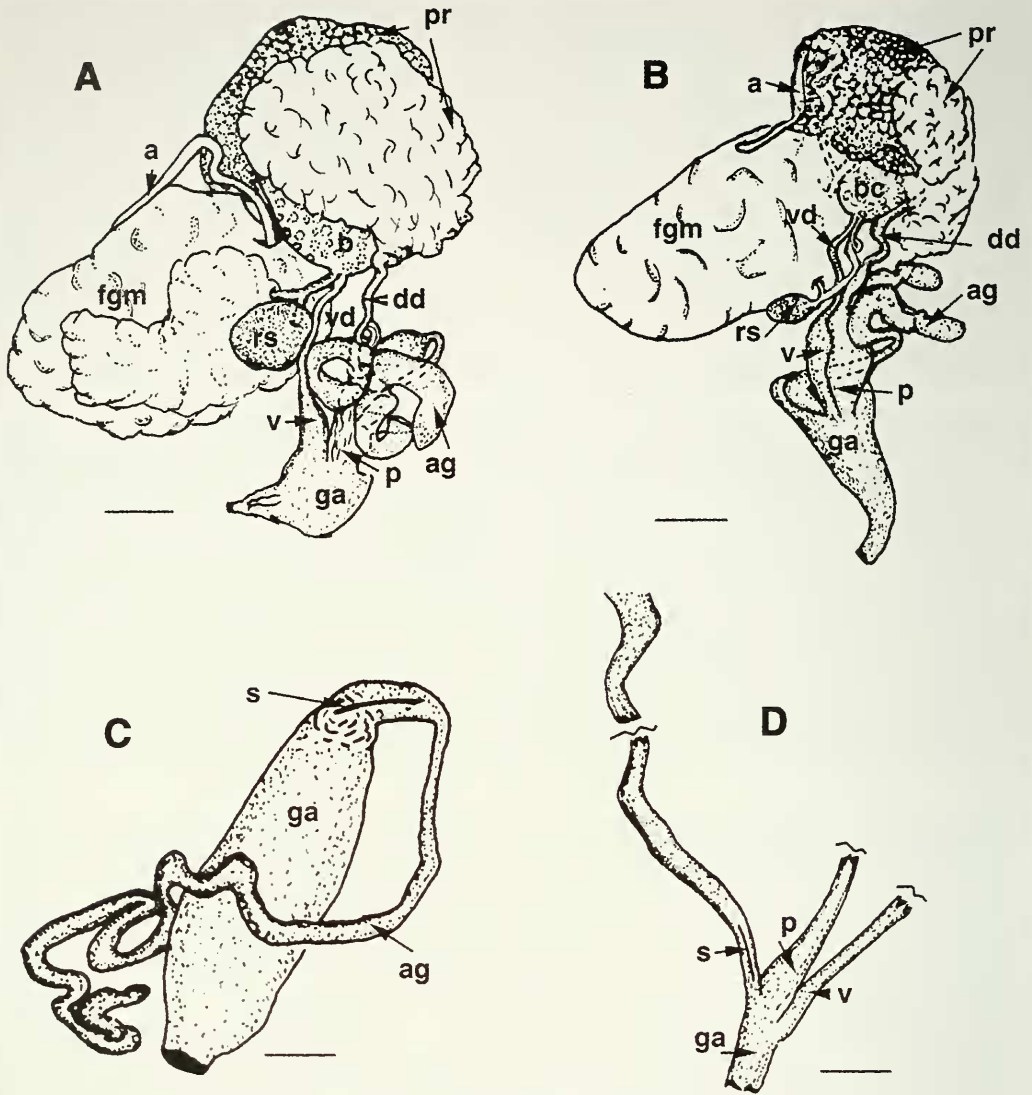


FIGURE 19. *Hoplodoris bifurcata* (CASIZ 070133)(CASIZ 087898) reproductive system. – A. Schematic drawing of entire reproductive system, Okinawa (CASIZ 070133). Scale bar = 1 mm. – B. Schematic drawing of entire reproductive system, Okinawa (CASIZ 087898). Scale bar = 1 mm. – C. Schematic expansion of CASIZ 070133. Scale bar = 0.5 mm. – D. Schematic expansion of CASIZ 087898. Scale bar = 0.5 mm. Abbreviations: a, ampulla; ag, accessory gland; bc, bursa copulatrix; dd, deferent duct; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; s, stylet (accessory gland); v, vagina; vd, vaginal duct.

inis at the base. This duct is moderately short and about the same length as the duct that connects the receptaculum to the bursa copulatrix. The spherical receptaculum seminis is much smaller than the bursa copulatrix, which is nearly the same size as the prostate. The bursa lies against the female gland mass and is partially encased by the prostate. The vaginal duct that emerges from the base of the bursa is not as long as the deferent duct, and is not looped. It widens into the vagina, which is not armed.

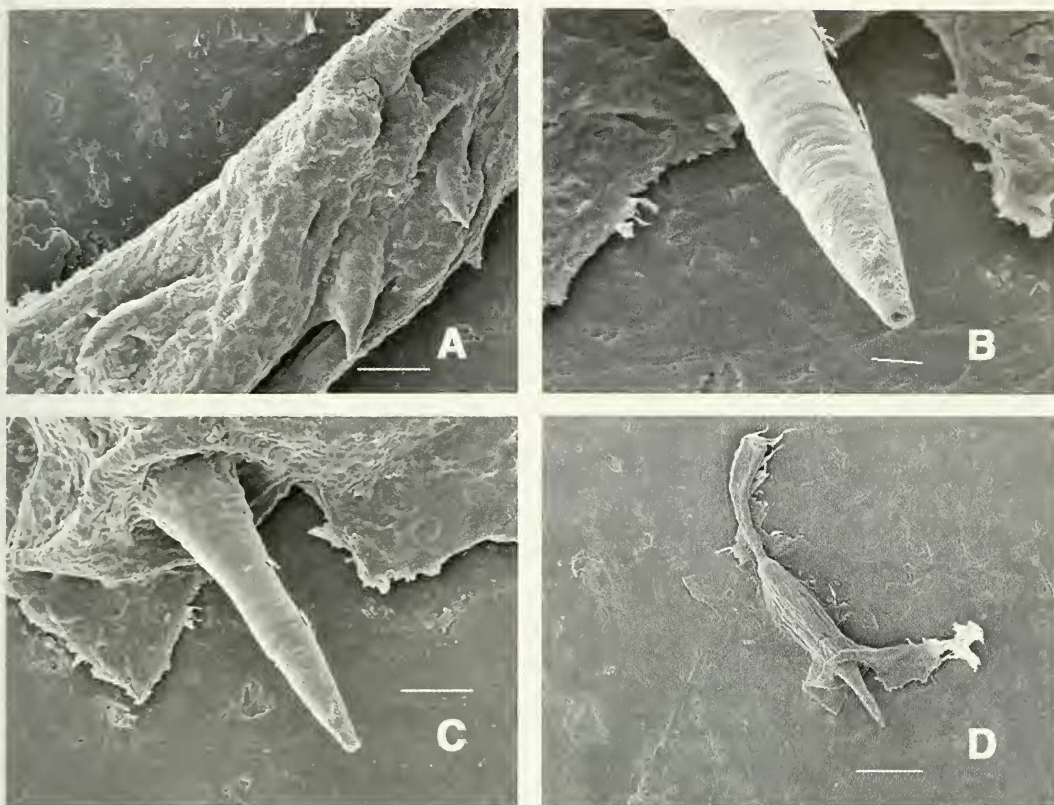


FIGURE 20. *Hoplodoris bifurcata* Hawaii (CASIZ 087898) genital armature. – A. Penial spines, close-up. Scale bar = 10 μ m. – B. Accessory gland stylet, close-up showing hollow tip. Scale bar = 10 μ m. – C. Accessory gland stylet, close-up. Scale bar = 100 μ m. – D. Entire accessory gland stylet. Scale bar = 100 μ m.

Alongside the vagina, at the genital atrium, is a large, bulbous vestibular gland. This gland has a convoluted, blind-ended, narrow duct terminating near the female gland mass (Figs. 19C–D). Inside the duct, near the junction of the muscular portion of the gland is a hollow stylet (Figs. 20B–D).

REMARKS.— Kay and Young (1969) described the anatomy of specimens they identified as *Carminodoris nodulosa* from Hawaii, but reported no armament on the penis, the vagina or in the vestibular gland. These structures were difficult to see in our examination of specimens from Hawaii and Okinawa. But the descriptions of the external morphology, the coloration and the radular features provided by Kay and Young are nearly identical to Baba's (1993) descriptions of *Carminodoris bifurcata* from Okinawa and differ from those of *C. nodulosa* from Australia and New Zealand.

Our specimens from Okinawa and Japan match Baba's original description of the external morphology and radula of *Carminodoris bifurcata*. However, Baba did not mention the presence of a vestibular gland armed with a stylet, nor did he provide a drawing of the entire reproductive system of this species.

From our examination of the specimens from Okinawa and Japan, it appears that Kay and Young's (1969) *Carminodoris nodulosa* from Hawaii and *Carminodoris bifurcata* are conspecific but quite distinct from other *Hoplodoris* species.

Debelius (1998) illustrated specimens of *Hoplodoris nodulosa* from Vietnam and Western Australia, but based on color pattern, these are *Hoplodoris estrelyado* Gosliner and Behrens, 1998.

Regarding *Hoplodoris estrelyado*, from our examination of *Hoplodoris* specimens, we can confirm that *H. estrelyado* is the only species of *Hoplodoris* that lacks both penial and vaginal armament. However, *Hoplodoris estrelyado* has one accessory gland stylet, as do all other species of *Hoplodoris* except *H. nodulosa* and *H. bramale*.

Hoplodoris nodulosa (Angas, 1864)

Figs. 17C, 21–23

= *Doris nodulosa* Angas, 1864.

= *Doris pustulosa* Abraham, 1877.

= *Honiodoris novaezelandiae* Bergh, 1904.

= *Doris novae-zelandiae* Suter, 1913:564.

= *Honiodoris novaezelandiae* Powell, 1946:90, Powell, 1979:286.

= *Staurodoris pustulata* (Abraham, 1877) in Allan, 1950.

= *Hoplodoris uodulosa* (Angas, 1864) in Thompson, 1975:491–492, figs. 1e, 3.

= *Hoplodoris uodulosa* (Angas, 1864) in Willan & Coleman, 1984:33, fig. 92.

= *Hoplodoris novaezelandiae* (Bergh, 1904) in Miller, 1991:295–303.

= *Hoplodoris uodulosa* (Angas, 1864) in Wells & Bryce, 1993:104, fig. 125.

MATERIAL EXAMINED.—C133935, one specimen, dissected, 26 mm, White Horse Point, Balmain, Sydney, Australia. Collected by I. Loch, 20 June 1982; C135412, two specimens, 15 and 23 mm, Sandy Beach, Coffs Harbour, New South Wales, Australia. Collected by G. Avern, 20 May 1982.

DISTRIBUTION.—This species is known from Eastern Australia (Angas 1864; Abraham 1877; Allan 1950; Thompson 1975; Willan and Coleman 1984; present study), from Western Australia (Wells and Bryce 1993) and from New Zealand (Bergh 1904; Powell 1946, 1979; Miller 1991).

EXTERNAL MORPHOLOGY.—The body of the living animal (Fig. 17C) is oval, flat and the notum is covered with large, round and tapered tubercles. The tubercles are mostly rounded on the dorsal median, becoming progressively smaller and more tapered around the median. The tubercles closest to the mantle edge are much smaller than the others. The coloration of the living animal is complex, and variegated. The ground color ranges from light to medium gray, to yellows and reddish-browns. Scattered over the mantle are mottled shades of darker hues of the major colors. On the central dorsum, is an oval of color that is more distinct than the surrounding coloration. The tubercles in this area all have the same coloration. On the tubercles towards the mantle edge, there can be a narrow, white ring at the base. Sprinkled randomly among the tubercles are tiny, dark brown or black spots. The long, tapered rhinophores are light tan at the base, with a darker tan or dark brown lamellar portion (approximately 32 lamellae) that angles posteriorly and terminates with a white tip. The six posteriorly projecting gill leaves are tripinnate and feathery and the anterior leaves are light tan with whitish flecks of color, while the posterior leaves can be a darker color similar to the central dorsal oval color. The rhinophore and gill sheaths are elevated and have tuberculate, irregular edges.

The ventral side of the specimens has retained no pigment. The oral tentacles are digitiform and the foot has a rounded notch on the anterior side.

BUCCAL ARMATURE (Fig. 21).—The buccal mass is large and muscular. At the anterior end of the muscular region is a thin, chitinous labial cuticle. The labial cuticle contains irregularly tipped jaw rodlets (Fig. 21A). The radular formula of the specimen dissected is: 25 × 53.0.53 (C133935).

The innermost lateral tooth is hamate with no denticles visible on either edge (Fig. 21B). The middle radular teeth have a more elongate cusp and are also smooth (Fig. 21C). The four outermost lateral teeth, particularly the last two teeth, are much shorter than the middle or inner teeth and are denticulate with fimbriate denticles (Fig. 21D).

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Fig. 22A). The ampulla is long and tubular and lies on top of the female gland mass and prostate gland. The ampulla narrows slightly into the postampullary duct, which bifurcates into the oviduct and vas deferens. The short oviduct enters the female gland mass. The long, tubular prostate narrows into a long, convoluted deferent duct. The prostate has two distinct glandular types that are differentially pigmented. The deferent duct continues into the bulbous penis, which lies next to the vagina. The penis is sparsely armed on the inside with short, thorn-like structures (Figs. 23A–B). Two bulbous accessory glands lie next to the penis and vagina. These glands have long, convoluted, blind-ended, narrow ducts that terminate next to the female gland mass (Figs. 22C–D). Inside the ducts, near the junction of the muscular portion of each gland is a hollow stylet (Figs. 23C–E).

The short uterine duct emerges from the female gland mass and joins the receptaculum seminis at the base. The pyriform receptaculum seminis is much smaller than the bursa copulatrix. The bursa lies against the female gland mass and is only barely covered by the prostate. The vaginal duct that emerges from the base of the bursa is not as long as the deferent duct, and is not looped. It widens into the vagina, which is not armed.

REMARKS.— Thompson's (1975) detailed description of the male reproductive organs of *Hoplodoris nodulosa* (Angas, 1864), includes an armed penis and non-hollow stylet inside a well-developed gland. We have examined three specimens from New South Wales that fit Thompson's description including the internal anatomy. In the specimen that Thompson examined, only the outer lateral teeth were denticulate, the same as we noted in the specimens from New South Wales that we examined. The specimens we examined had two hollow stylets versus a single "non-tubular" stylet described by Thompson. However, without a scanning electron microscope, the hole in the end of the stylet would have been overlooked.

Miller (1991) described several specimens from New Zealand as *Hoplodoris novaezelandiae* (Bergh, 1904). His description matches the specimens we examined from New South Wales, Australia. Based on a review of Bergh's original (1904) description of *Hoplodoris novaezelandiae*, of Miller's (1991) description of specimens from New Zealand, and our examination of specimens from and near the type locality of *Hoplodoris nodulosa* (Angas, 1864), we conclude that *Hoplodoris novaezelandiae* and *Hoplodoris nodulosa* are conspecific.

The specimens of *H. nodulosa* that we examined from the type locality in New South Wales have an armed penis and two well-developed accessory glands, each containing a hollow stylet. In addition, the four outer lateral teeth of these specimens are fimbriate.

Hoplodoris estrelyado Gosliner & Behrens, 1998

Fig. 24

(See Gosliner and Behrens, 1998:280–286 for complete synonymy and anatomy.)

= *Hoplodoris nodulosa* (Angas, 1864) misidentification in Debelius, 1998:253, bottom figures.

MATERIAL EXAMINED.— CASIZ 115343, two specimens, dissected, 40 mm. Devil's Point, Maricaban, Batangas Province, Philippine Islands. Collected by T.M. Gosliner, 15 April 1996.

DISTRIBUTION.— This species is known from the Philippine Islands (Gosliner and Behrens 1998; present study), Western Australia (Debelius 1998), Vietnam (Debelius 1998), Indonesia, Marshall Islands, Solomon Islands and the Coral Sea.

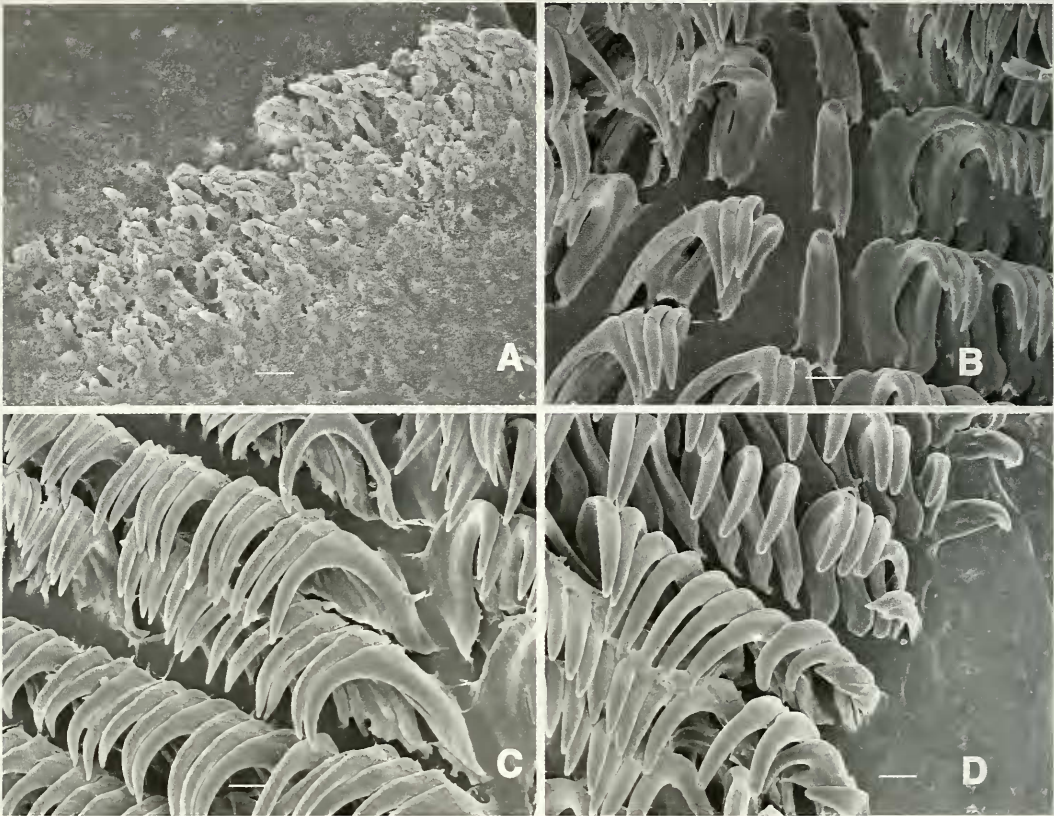


FIGURE 21. *Hoplodoris nodulosa* New South Wales (C135412).— A. Labial rods. Scale bar = 2 μ m. — B. Inner lateral teeth. Scale bar = 300 μ m. — C. Middle lateral teeth. Scale bar = 300 μ m. — D. Outer lateral teeth. Scale bar = 20 μ m.

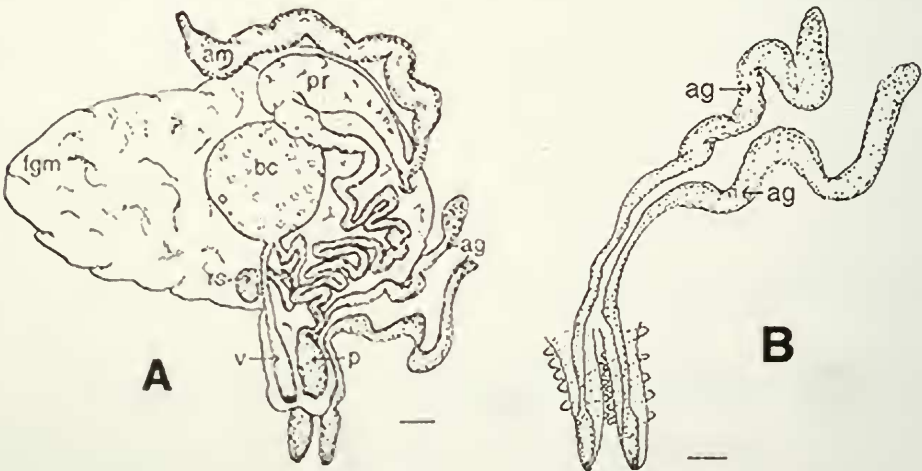


FIGURE 22. *Hoplodoris nodulosa* New South Wales (C133935). — A. Schematic drawing of entire reproductive system. Scale bar = 1 mm. — B. Schematic expansion of accessory glands. Scale bar = 0.5 mm.

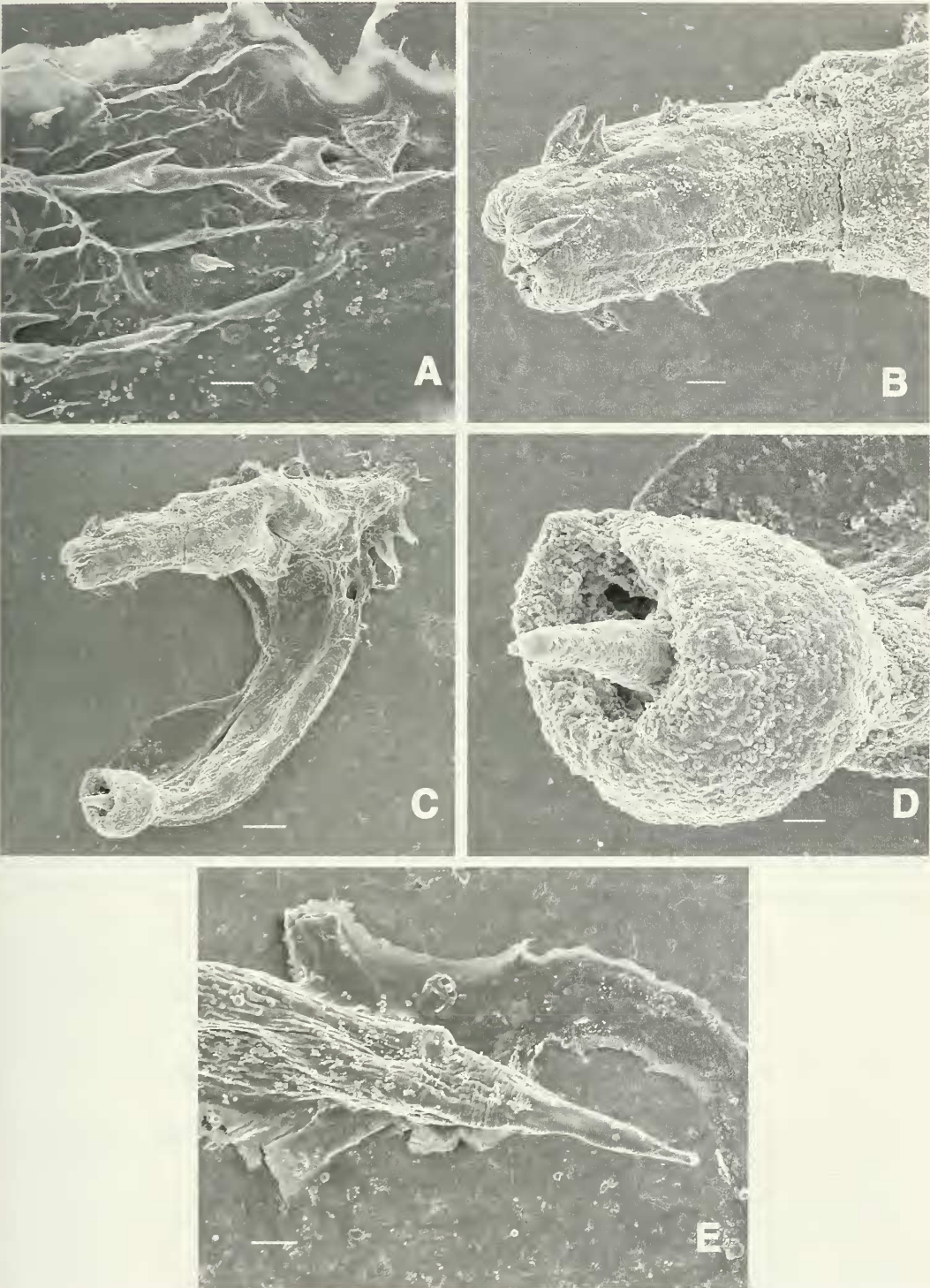


FIGURE 23. *Hoplodoris nodulosa* New South Wales (C133935). – A. Penial armament. Scale bar = 100 μ m. – B. Penial spines, close-up. Scale bar = 80 μ m. – C. Accessory gland stylet. Scale bar = 300 μ m. – D. Accessory gland stylet, close-up. Scale bar = 100 μ m. – E. Second accessory stylet, close-up. Scale bar = 100 μ m.

EXTERNAL AND RADULAR MORPHOLOGY.— The specimens examined conform to the external and radular morphology descriptions in Gosliner and Behrens.

REPRODUCTIVE SYSTEM.— The specimens examined conform to the reproductive morphology described by Gosliner and Behrens. The accessory gland spine (stylet) depicted by Gosliner and Behrens (1998, fig. 2) was also observed in the specimens examined for this study (Fig. 24). Observations by scanning electron microscopy also confirmed that neither the penis nor vagina is armed.

REMARKS.— The specimens of *Hoplodoris estrelyado* we examined for the present study match the original description of the radular and reproductive morphology (Gosliner & Behrens 1998). We can also clarify three points made in the discussion section of that publication, wherein comparison is made between *H. estrelyado* and other species of *Hoplodoris*. First, our examination of multiple *Hoplodoris* specimens revealed that *H. estrelyado* is not the only species of *Hoplodoris* in which all teeth are denticulate. All teeth of *H. bifurcata* specimens that we examined are also denticulate.

The second point is that *C. grandiflora* does have an armed penis as opposed to the Gosliner and Behrens (1998) observation that only *H. (C.) grandiflora* (Pease, 1860) and *H. estrelyado* have an unarmed penis. This detail is further considered in the remarks section of the present study where details of *H. grandiflora*, *C. mauritiana* and *H. desmoparypha* are described.

Lastly, neither *H. nodulosa* nor *H. estrelyado* have a solid stylet. Our electron microscopy examinations of the spines from both species revealed a hollow stylet.

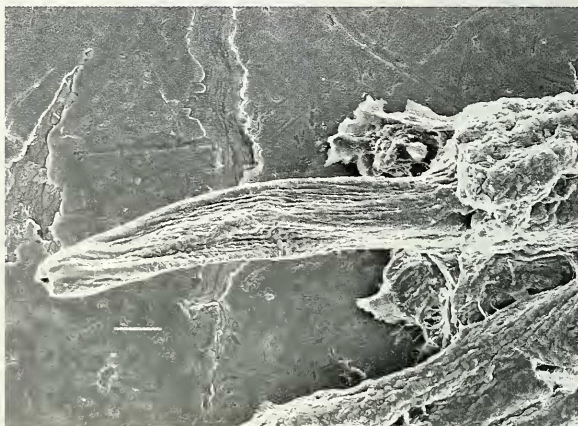


FIGURE 24. *Hoplodoris estrelyado* Philippines (CASIZ 115343). — A. Accessory gland stylet, showing hollow tip. Scale bar = 100 μ m.

***Hoplodoris flammea* Fahey and Gosliner, sp. nov.**

Figs. 17D, 25–27

MATERIAL EXAMINED.— **HOLOTYPE:** CASIZ 139600, one specimen, 12 mm, Tulamben, Bali, Indonesia. Collected by T.M. Gosliner, 31 October 2000. **PARATYPES:** CASIZ 140345, one specimen, dissected, 22 mm, Tulamben, Bali, Indonesia. Collected by T.M. Gosliner, 31 October 2000. CASIZ 140350, one specimen, 10 mm, Tulamben, Bali, Indonesia. Collected by T.M. Gosliner, 31 October 2000. CASIZ 162234, one specimen, dissected, 24 mm, Tulamben, Bali, Indonesia. Collected by T.M. Gosliner, 31 October 2000.

DISTRIBUTION.— This species has so far been found only in Bali, Indonesia (present study).

ETYMOLOGY.— The specific name *flammea* is from the Latin meaning fiery red, the dorsal median color of this species.

EXTERNAL MORPHOLOGY (Fig. 17D).— The preserved animals range from 22–24 mm in length. The body is oval, flat and the notum is covered with large, rounded tubercles. The coloration of the living animal is complex, and variegated. The ground color is a light to medium, reddish-mottled brown or tan. In the center of the dorsum the tubercles are bright red, with white areas

around them. At the base of the tubercles closer to the mantle edge, is the same white ring-like coloration around the evenly spaced clumps of smaller tubercles. Along the mantle edge are evenly spaced patches of reddish-brown tubercles. On the knobby tops of some of the brown tubercles, the coloration appears worn off and white coloration is visible. The close-set, tall rhinophores have approximately 16 lamellae and a light tan stalk with brown pigment circling the upper third of the stalk. The tip is white. The six tripinnate gill leaves are feathery and colored light gray with tan tips. The rhinophore and gill sheaths are raised with irregular edges and have small rounded tubercles on the sides and the rim.

The foot is notched anteriorly and the oral tentacles are digitiform. No coloration has been retained on the ventral side of the specimens examined.

BUCCAL ARMATURE.—The buccal mass is large and muscular. At the anterior end of the muscular region is a thin, chitinous labial cuticle. The labial cuticle contains irregularly tipped jaw rodlets that have distinct knurls along the length (Figs. 25A–B). The radular formula of the specimen examined is: $31 \times 50.0.50$ (CASIZ 140345). The innermost lateral teeth of both specimens dissected are hamate with the innermost tooth having a short secondary cusp on the inner edge next to the primary cusp (Figs. 25C–D). The middle radular teeth are also hamate, with a longer cusp (Fig. 25E) with about 8 denticles along the outer margin of the cusp. The five outermost lateral teeth have minute, feathery denticles on the outer edge and are smaller than the middle and inner lateral teeth (Fig. 25F).

REPRODUCTIVE SYSTEM.—The reproductive system is triaulic (Fig. 26). The ampulla is long, thin and tubular and lies between the female gland mass and prostate gland. The ampulla narrows slightly into the postampullary duct, which bifurcates into the oviduct and vas deferens. The short oviduct enters the female gland mass. The tubular prostate narrows into a medium length deferent duct. The prostate has two distinct glandular types that are differentially pigmented. The deferent duct then widens into the penial bulb, which lies next to the narrow vagina. The penis, which is armed with sparsely scattered hooks (Figs. 27A–B) is wider than the vagina and opens into the common genital atrium.

The short uterine duct emerges from the female gland mass and joins the receptaculum seminis at the base. This duct is moderately short and about the same length as the duct that connects the receptaculum to the bursa copulatrix. The spherical receptaculum seminis is about half the size of the bursa copulatrix. The bursa lies against the female gland mass and is not encased by the prostate. The vaginal duct that emerges from the base of the bursa is not as long as the deferent duct, and is not looped. The duct terminates into the vagina, which is not armed. A bulbous accessory gland opens into the genital atrium. The gland has a convoluted, blind-ended, narrow duct terminating near the female gland mass (Fig. 26). Inside the duct, near the junction of the muscular portion of the gland is a hollow stylet (Figs. 27C–D).

COMPARISON OF *HOPLODORIS FLAMMEA* TO OTHER *HOPLODORIS* SPECIES

Hoplodoris flammea is superficially similar to *H. bifurcata*. Both species have a central dorsum color that is distinct from the surrounding mantle coloration. *Hoplodoris flammea* has a bright red color, while the central color of *H. bifurcata* is more reddish-brown. Both species have complex, variegated coloration with mottled shades of grays and browns. Both have elongate rhinophores with deep tan lamellar regions and white tips. The gill leaves of both species are feathery and tan in color. But, *Hoplodoris flammea* lacks the small black spots on the notum that are present in *H. bifurcata*. Further, the interior anatomy, particularly the radular morphology, differs between these species. The inner lateral teeth of *Hoplodoris flammea* have a blunt cusp on the inner

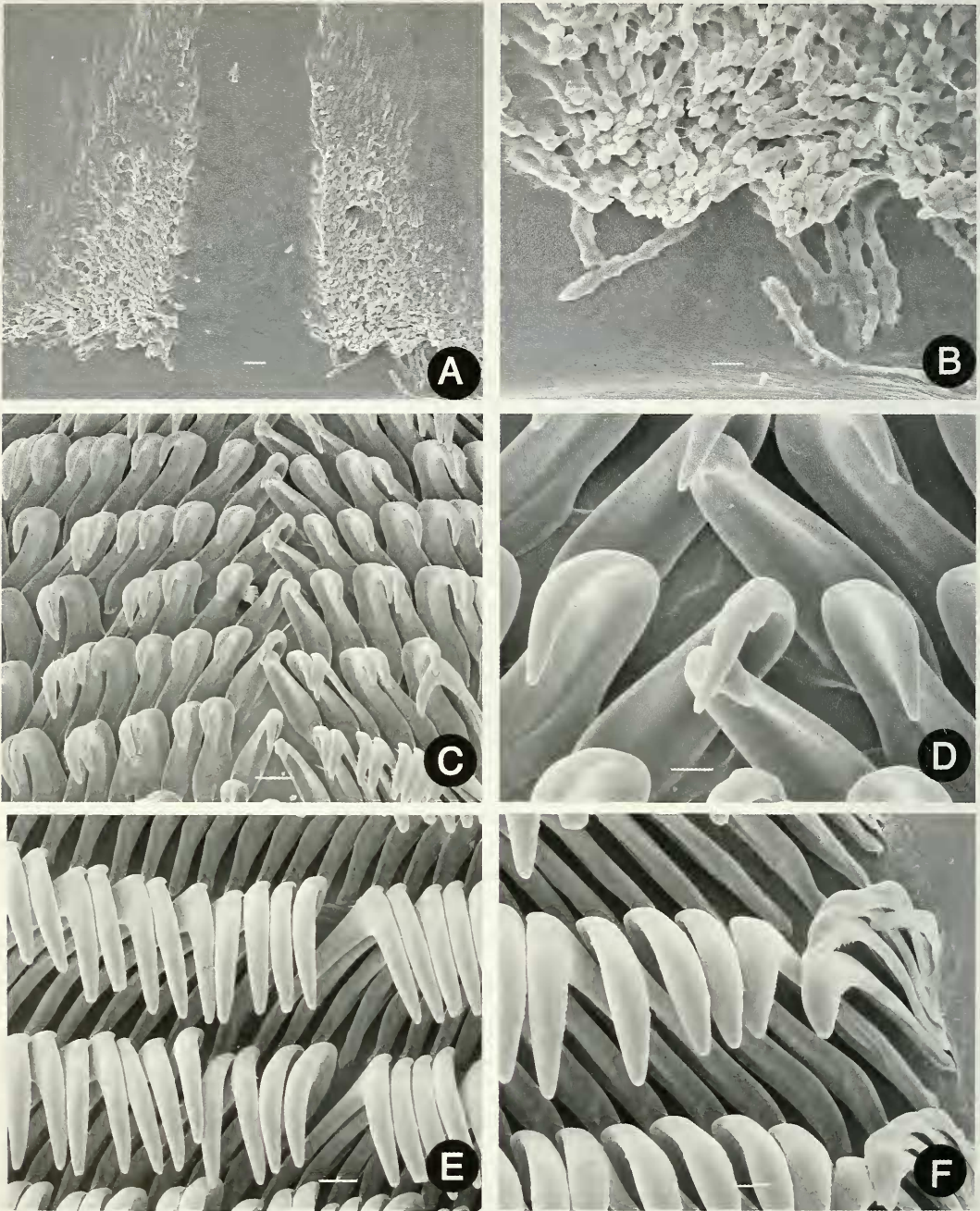


FIGURE 25. *Hoplodoris flammea* Bali (CASIZ 140345). – A. Labial rods. Scale bar = 1 µm. – B. Labial rods, close-up. Scale bar = 10 µm. – C. Inner lateral teeth. Scale bar = 100 µm. – D. Inner lateral teeth, close-up. Scale bar = 10 µm. – E. Middle lateral teeth. Scale bar = 15 µm. – F. Outer lateral teeth. Scale bar = 10 µm.

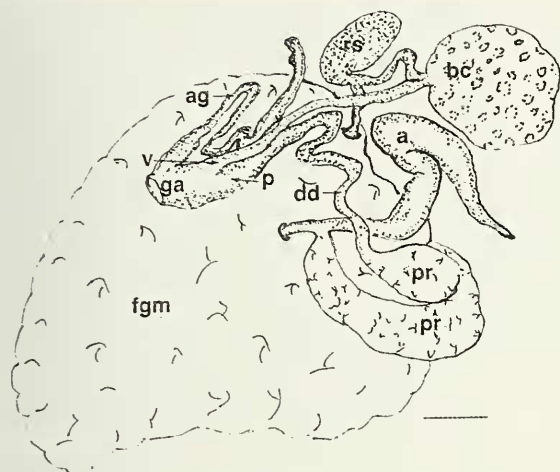


FIGURE 26. *Hoplodoris flammea* Bali (CASIZ 140345). Schematic drawing of entire reproductive system. Scale bar = 1 mm.

edge, while the inner lateral teeth of *H. bifurcata* have denticles on both the inner and outer edges of the innermost lateral tooth. The middle and outer lateral teeth of both species are denticulate, but the denticles of the middle lateral teeth of *H. bifurcata* are more pronounced. *Hoplodoris bifurcata* has three denticulate outer lateral teeth while *H. flammea* has four denticulate outer lateral teeth that are more brush-like. The jaw rodlets of *H. flammea* also differ in that they have distinct knobs along the length. The jaw rodlets of *H. bifurcata* are flattened plates with blunt ends.

The differences in the reproductive anatomy between the two species are as follows: the prostate of *Hoplodoris flammea* is a thick coil that does not cover the

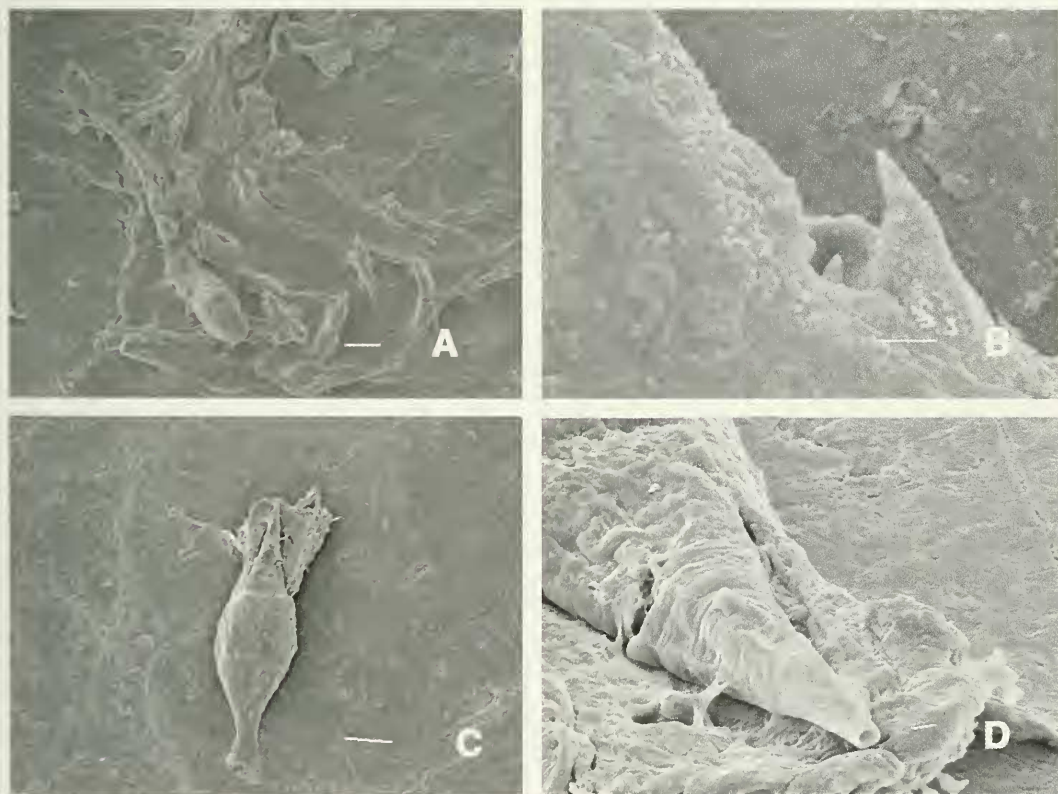


Figure 27. *Hoplodoris flammea* Bali (CASIZ 140345). – A. Penial armament. Scale bar = 100 μ m. – B. Penial spines, close-up. Scale bar = 10 μ m. – C. Accessory gland stylet. Scale bar = 10 μ m. – D. Accessory gland stylet, close-up. Scale bar = 1 μ m.

bursa copulatrix. The prostate of *H. bifurcata* covers the bursa and is a large mass rather than a coiled tube. The vagina of *H. flammea* is shorter than the deferent duct, but in *H. bifurcata* the vagina is longer than the deferent duct.

Thus, a combination of morphological characters distinguishes *H. flammea* as a separate *Hoplodoris* species.

***Hoplodoris bramale* Fahey and Gosliner, sp. nov.**

Figs. 17E, 28–30

MATERIAL EXAMINED.—HOLOTYPE: INB 0003572316, 24 mm, Puerto Escondido, Parque Nacional Manuel Antonio, Puntarenas, Costa Rica. Intertidal. Collected by Y. Camacho-Garcia, 18 February 2003. PARATYPES: INB 0001498550, one specimen, dissected, 22 mm, Tómbolo, Punta Uvita, Osa Conservation Area, Costa Rica. Intertidal. Collected by Y. Camacho-García and D. Butvill, 6 January 2002. Two specimens (CASIZ 166813). Punta Uvita, Osa Conservation Area, Pacific coast of Costa Rica, 0–2 m depth, 15 January 2003. One specimen (CASIZ) Punta Uvita, Osa Conservation Area, Pacific coast of Costa Rica, 0–2 m depth, 15 January 2003. Six specimens (INB 0003572306) Punta Uvita, Ballena National Park, Pacific coast of Costa Rica, 0–2 m depth, 18 January 2003.

DISTRIBUTION.— This species is known only from the Pacific coast of Costa Rica. It appears to be the only species of *Hoplodoris* found in the Eastern Pacific.

ETYMOLOGY.— The specific name *bramale* is taken from the Latin “tuber bramale” a name given to a truffle that has the same appearance as this new species.

EXTERNAL MORPHOLOGY (Fig. 17E).— The preserved animal measures 22 mm. The body is oval, flat and the notum is covered with large, rounded tubercles. The coloration of the living animal is complex and variegated. The ground color is light to medium mottled brown or tan. At the base of the tubercles is a white area in the shape of a ring. Alongside the medial part of the dorsum are the tallest tubercles. In the middle of the dorsum, the white area decreases at the base of some tubercles, and the tubercles are shorter than those alongside the median. Along the mantle edge the tubercles are small and more densely packed than on the dorsum median. The close-set, stout rhinophores have a medium brown stalk with a lighter brown lamellar portion (approximately 10–13 lamellae) that terminates with a white tip. The six tripinnate gill leaves are feathery and light tan in color. The rhinophore and gill sheaths are low with irregular edges and have small rounded tubercles on the sides.

The foot is notched anteriorly and the oral tentacles are digitiform. Some dark speckles have been retained on the ventral side of the specimens examined.

BUCCAL ARMATURE.— The buccal mass is large and muscular. At the anterior end of the muscular region is a thin, chitinous labial cuticle. The labial cuticle contains irregularly tipped jaw rodlets that have rough, irregular edges (Figs. 28A–B). The radular formula of the specimen examined is: 28 × 38.0.38. The innermost lateral teeth are hamate and narrow below the cusp (Fig. 28C). The cusp is devoid of denticles on either side. The middle radular teeth are also hamate, with a longer cusp (Fig. 28D) and lack denticles. The two outermost lateral teeth have fine denticles on the outer edge and are smaller than the middle and inner lateral teeth (Figs. 28E–F).

REPRODUCTIVE SYSTEM.— The reproductive system is triaullc (Fig. 29A). The ampulla is long, thin and tubular and lies between the female gland mass and prostate gland. The ampulla narrows slightly into the postampullary duct, which bifurcates into the oviduct and vas deferens. The short oviduct enters the female gland mass. The long, tubular prostate narrows into a long, looped deferent duct. The prostate has two distinct glandular types that are differentially pigmented. The deferent duct continues into the thin penis, which lies between two bulbous accessory glands.

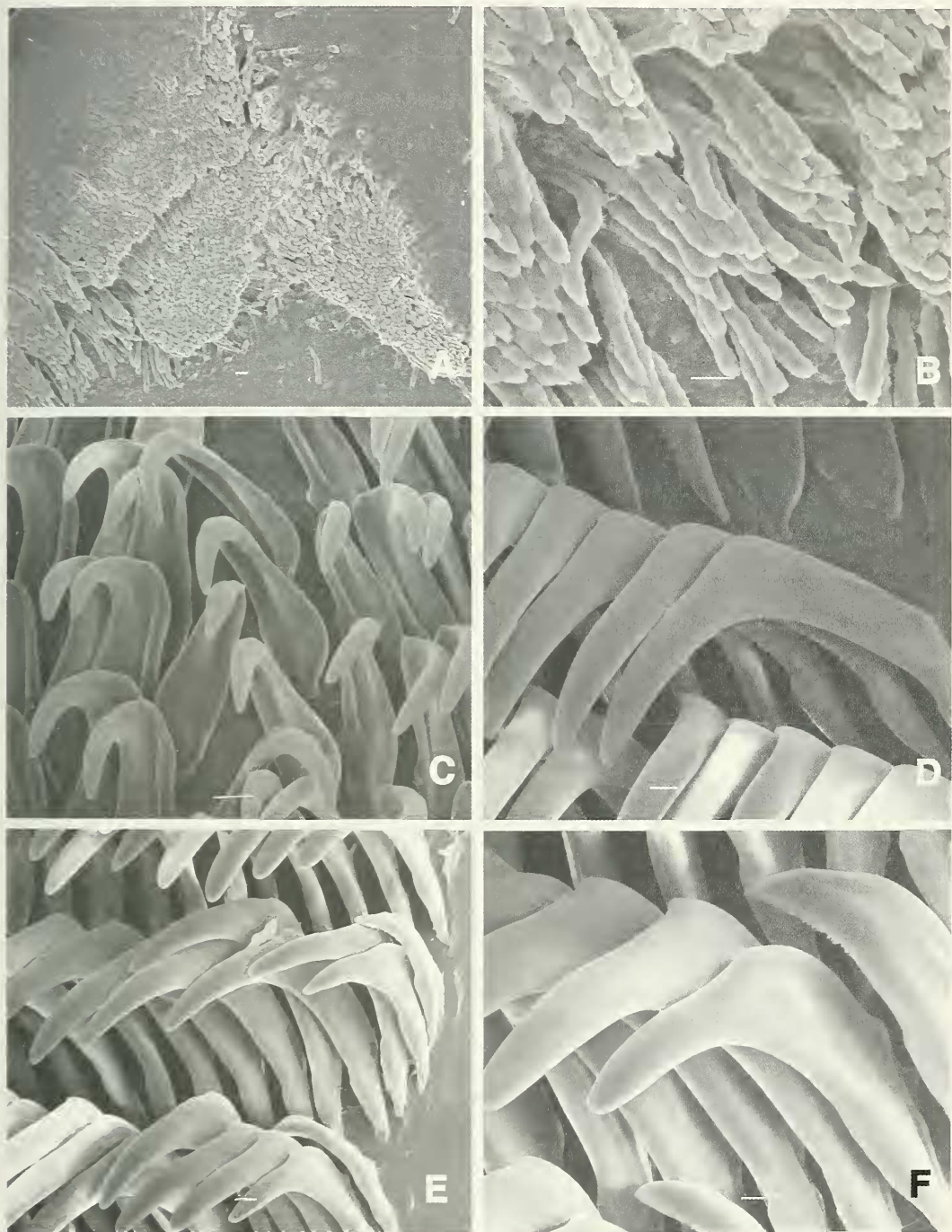


FIGURE 28. *Hoplodoris bramale* Costa Rica (INB 0001498550). – A. Labial rods. Scale bar = 10 μ m. – B. Labial rods, close-up. Scale bar = 10 μ m. – C. Inner lateral teeth. Scale bar = 300 μ m. – D. Middle lateral teeth, close-up. Scale bar = 25 μ m. – E. Outer lateral teeth. Scale bar = 10 μ m. – F. Outer lateral teeth, close-up. Scale bar = 1 μ m.

These glands have long, convoluted, blind-ended, narrow ducts that terminate near the female gland mass (Fig. 29B). Inside the ducts, near the junction of the muscular portion of each gland is a hollow stylet (Figs. 30A–B). The penis is sparsely armed on the inside with short, thorn-like structures. (Fig. 30C).

The short uterine duct emerges from the female gland mass and joins the receptaculum seminis at the base. This duct is moderately short and about the same length as the duct that connects the receptaculum to the bursa copulatrix. The spherical receptaculum seminis is about the same size as the bursa copulatrix. The bursa lies against the female gland mass and is partially encased by the prostate. The vaginal duct that emerges from the base of the bursa is not as long as the deferent duct, and is not looped. It widens into the vagina, which is not armed.

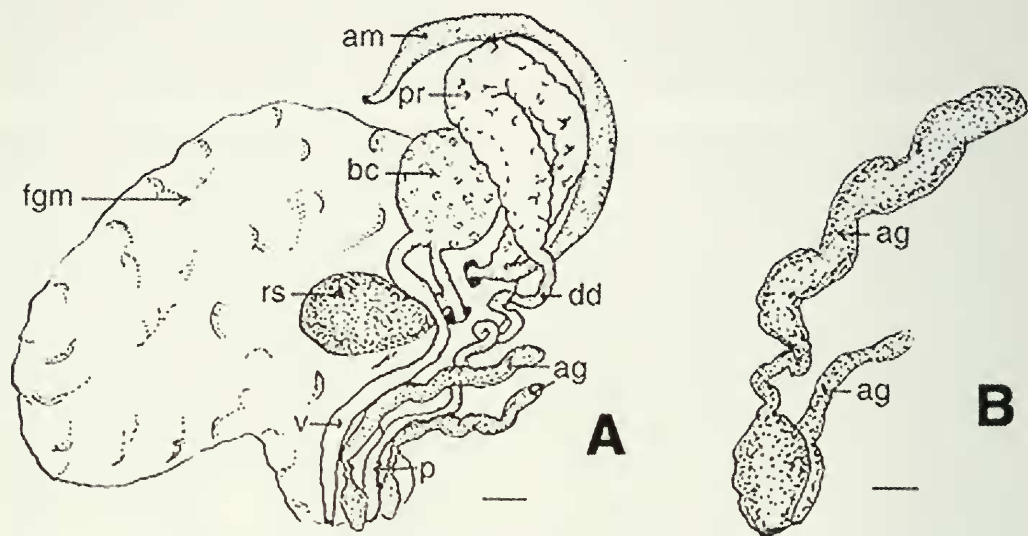


FIGURE 29. *Hoplodoris bramale* Costa Rica (INB 0001498550).— A. Schematic drawing of entire reproductive system. Scale bar = 1 mm. — B. Schematic expansion of accessory gland. Scale bar = 0.5 mm.

COMPARISON OF *H. BRAMALE* TO OTHER *HOPLODORIS* SPECIES

Hoplodoris bramale is most similar externally to *H. grandiflora*. The notum of both species is brown, with no distinctive central oval of color. Both species have brown tubercles surrounded by a white ring at the base. The brown rhinophores have a white tip and a raised rhinophore sheath. The feathery gill leaves are light brown or tan. The gill sheath of both species is covered with small tubercles.

Differences in the internal anatomy distinguish the two species. Although the 3–4 outer lateral teeth of *Hoplodoris grandiflora* have minute denticles and are smaller than the middle lateral teeth, *H. bramale* has only one to two smaller outer lateral teeth with tiny denticles. Additionally, the middle lateral teeth of *H. bramale* have longer hooks and lack denticles while those of *H. grandiflora* are shorter and denticulate. The inner lateral teeth of both species are hamate and *H. bramale* differs by having a small, blunt cusp on the innermost tooth.

The reproductive anatomy of the two species varies considerably. *Hoplodoris bramale* has two armed accessory glands while *H. grandiflora* has one gland.

Internally, *Hoplodoris bramale* is most similar to *H. nodulosa* (Angas, 1864). *Hoplodoris*

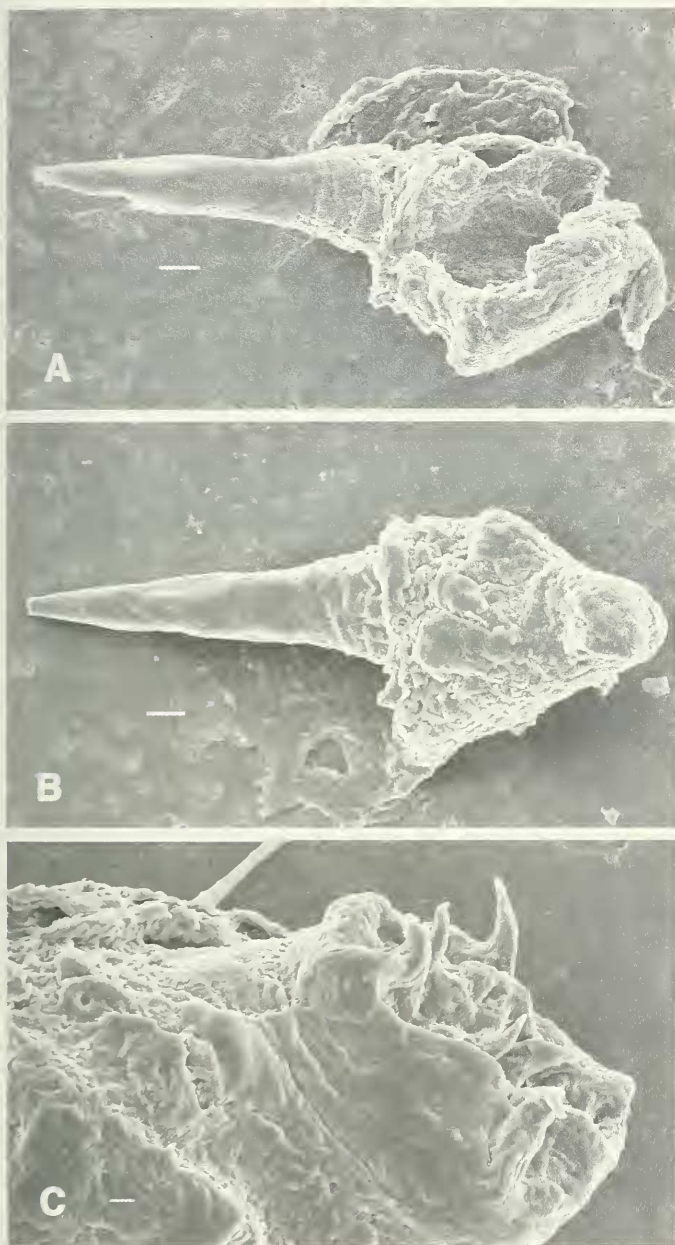


FIGURE 30. *Hoplodoris bramale* Costa Rica (INB 0001498550). - A. Accessory gland stylet, close-up. Scale bar = 100 μ m. - B. Second accessory stylet, close-up. Scale bar = 100 μ m. - C. Penial armament. Scale bar = 5 μ m.

nodulosa also has two accessory glands but in that species, the penis does not lie between the two glands as it does in *H. bramale*. The penis of *H. bramale* is sparsely armed with short thorn-like spines as in *H. nodulosa*, while the penis of *H. grandiflora* is densely armed. The vagina of *H. bramale* is not armed; also similar to *H. nodulosa*, but the vagina of *H. grandiflora* is armed. The deferent duct of *H. bramale* is not as elongate and coiled as that of *H. grandiflora* or *H. nodulosa*. The receptaculum seminis of both *H. bramale* and *H. grandiflora* is nearly the same size as the bursa, but in *H. nodulosa* the receptaculum is much smaller than the bursa.

Externally, *Hoplodoris bramale* is quite different from *H. nodulosa*. The dark oval of coloration on the dorsum of *H. nodulosa* is not found on *H. bramale*. In addition, *H. bramale* lacks the small black spots on the notum that are generally present in *H. nodulosa*.

The particular combination of morphological characters distinguishes *Hoplodoris bramale* from other species of *Hoplodoris*.

PHYLOGENTIC ANALYSIS

To test our hypothesis of phylogenetic relationships, we assessed the characters that could be informative. From our study, it appears that there are few characters that can be used to distinguish among these closely related taxa. For example, there are few external morphological characters that can be incorporated into phylogenetic analyses. There are also few reproductive or radular differences that can be used to distinguish between taxa.

CHARACTERS.—The following characters were considered for use in the analyses of *Hoplodoris* and *Carminodoris*. The character states are 0 = plesiomorphic condition, 1, 2 = apomorphic conditions. None of the character states was determined *a priori*; the result of examination of the outgroup character states. The outgroup selected, *Discodoris boholiensis* Bergh, 1877 is the type species of the genus. *Geitodoris planata*, the type species of the genus *Geitodoris* Bergh, 1894, was included in the ingroup to test the monophyly of *Hoplodoris* and *Carminodoris*. Phylogenetic analyses performed by Valdés (2002) demonstrate that both *Discodoris* and *Geitodoris* are more basally situated than *Hoplodoris*, but are nonetheless closely related. When available, we determined the character state for the taxon by examination of specimens in the California Academy of Sciences and Australian Museum collections, rather than relying on literature descriptions. Only *Carminodoris armata* Baba, 1993 was unavailable for examination.

1. *Vas deferens shape*. Both *Discodoris* and *Geitodoris* have a very long, convoluted vas deferens (0). This state is shared by the majority of *Hoplodoris* species except *H. armata*, *H. bifurcata*, *H. flammea* and *H. bramale*, which all have a shorter, although convoluted duct (1).

2. *Penial armature*. The outgroup lacks penial hooks or other armature (0), as does *Geitodoris planata* and *H. estrelyado*. All other species have penial armature (1).

3. *Vaginal armature*. *H. grandiflora*, *H. mauritiana*, *H. desmoparypha* each has an armed vagina (1).

4. *Vestibular gland*. *Discodoris* does not have a vestibular gland attached to or near the genital atrium (0). However, *Geitodoris* and all species of *Hoplodoris* and *Carminodoris* have a vestibular gland (1). Two species have two of these vestibular glands attached near the genital atrium (2), *H. nodulosa* and *H. bramale*.

5. *Vestibular gland duct*. The vestibular gland duct in *Geitodoris* is narrow, (0). All species share this state, except *H. estrelyado* and *H. armata*, which have a wide vestibular gland (1).

6. *Penis shape*. Members of the outgroup and *Geitodoris* have a wide, bulbous penis (0), as do most *Hoplodoris* species. Both *H. estrelyado* and *H. bramale* have a narrow penis (1).

7. *Stylet*. Neither *Discodoris* nor *Geitodoris* has armature (a stylet) associated with an assessor gland (0). All species of *Hoplodoris* examined in this study have a stylet (1).

8. *Stylet number*. Neither *Discodoris* nor *Geitodoris* has a stylet, so this character state is coded as inapplicable (?). All but one species of *Hoplodoris* have one stylet (0), and *Hoplodoris nodulosa* and *H. bramale* have two stylets (1).

9. *Outer lateral teeth*. The outer lateral teeth of *Discodoris* are not denticulate (0). This character state is shared by *Hoplodoris armata*. All other species have denticulate outer laterals (1).

10. *Middle lateral teeth*. Neither *Discodoris* nor *Geitodoris* have denticulate middle lateral teeth (0). Five species share this state. All other species have denticulate middle lateral teeth (1). This character was left out of the final analysis when examination of multiple specimens revealed intraspecific variation.

11. *Inner lateral teeth*. Neither outgroup has denticulate inner lateral teeth (0). Of the ingroup taxa, five have denticulate inner lateral teeth (1). This character was left out of the final analysis when examination of multiple specimens revealed intraspecific variation.

12. *Dorsal tubercle form*. Both *Discodoris* and *Geitodoris* have conical, small tubercles covering the dorsum (0). In contrast, the members of *Hoplodoris* and *Carminodoris* have prominent, rounded and tapered tubercles (1).
13. *Dorsal color*. Both *Discodoris* and *Geitodoris* have uniform dorsal coloration, which is not concentrated in the center (0). This character state is shared by most species. Three species, *H. bifurcata*, *H. nodulosa* and *H. flammea* have a dark median coloration (1).
14. *Penial spine density*. Of the species having a penial spine, four have densely spaced spines (0) and four have sparsely distributed spines (1).

PHYLOGENETIC ANALYSIS.— In order to perform analyses of phylogeny, character state data were entered into a data matrix using MacClade version 4.0 (Table 1). Phylogenetic Analysis Using Parsimony (PAUP) version 4.0b10 was used to analyze the data. The optimality criterion of maximum parsimony, with the heuristic algorithm (TBR branch swapping option) was used. Multistate characters were treated as unordered with equal weight and the stepwise addition option of random trees was used with 100 repetitions for the maximum parsimony.

Bremer analyses were performed to estimate branch support. A 50% majority rule consensus tree was computed for all trees. Permutation Tests for Probability (PTP) were performed to determine if a tree as short as that found from parsimony analysis could have arisen by chance alone. Skewness tests, with evaluation of 100,000 and 1 million random trees, were performed to evaluate whether the data set contains more hierarchical structure than would be expected by chance.

RESULTS.— For the analyses using maximum parsimony as an optimality criterion, eight equally parsimonious trees were found, which were 19 steps long. Tree scores were as follows: the consistency index (CI) = 0.68, retention index (RI) = 0.70 and homoplasy index (HI) = 0.32. The strict consensus tree is shown in Fig. 31A with the character numbers and character reversals. The underlined number indicated a reversal. The 50% majority rule tree is shown in Fig. 31B. The evaluation of the randomly sampled trees for the skewness test resulted in a mean of 30.2, a standard deviation of 1.77, a g1 value of -0.72 and a g2 value of 0.51.

Bremer support analyses conducted using heuristic searches by PAUP for all trees ≤ 20 , ≤ 21 , ≤ 23 and ≤ 24 steps resulted in 92, 658, 3324 and 13024 trees respectively. Bremer support values are shown on Fig. 31A. *Discodoris boholiensis* remained separated from the *Hoplodoris* clade even after analysis of ≤ 25 steps.

TABLE 1. *Hoplodoris* data matrix

Species	Characters (see text)													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 <i>H. armata</i>	1	1	0	2	1	0	?	?	0	0	0	1	0	0
1 <i>H. armata</i>	1	1	0	2	1	0	?	?	0	0	0	1	0	0
3 <i>H. grandiflora</i>	0	1	1	1	0	0	1	0	1	1	1	1	0	0
4 <i>H. mauritiana</i>	0	1	1	1	0	0	1	0	1	1	1	1	0	0
5 <i>H. nodulosa</i> Aust	0	1	0	2	0	0	1	1	1	0	0	1	1	1
6 <i>H. desmoparypha</i>	0	1	1	1	0	0	1	0	1	0	0	1	0	0
7 <i>H. estreylado</i>	0	0	0	1	1	1	1	0	1	1	1	1	0	?
8 <i>H. flammea</i>	1	1	0	1	0	0	1	0	1	0	1	1	1	1
9 <i>H. bramale</i>	1	1	0	2	0	1	1	1	1	0	0	1	0	1
10 <i>D. boholiensis</i>	0	0	0	0	?	0	0	?	0	0	0	0	0	?
11 <i>G. planata</i>	0	0	0	1	0	0	0	?	1	0	0	0	0	?

DISCUSSION OF PHYLOGENETIC ANALYSES.—The results of these phylogenetic analyses are consistent with the recent analyses and opinions of other authors (Gosliner and Behrens 1998; Thompson 1975). First, the present analysis supports the opinion of these authors that *Carminodoris* is a junior synonym of *Hoplodoris*. However, neither taxon appears monophyletic. Instead, all species previously placed in *Carminodoris* and *Hoplodoris* appear to be members of one clade (Fig. 30). PTP tests ($P = 0.01$) indicate that a tree length of 19 steps is significantly shorter than randomly generated trees. The PTP tests generated the shortest trees of 26 steps. The retention index of 0.70 for the parsimony tree demonstrates strong statistical fit of the characters to the tree (G. Spicer, pers. commun.). The results of the randomly sampled trees, in particular the gl value of -0.72, indicated that the data is significantly more structured than random data.

Regarding the outgroups selected for this study, Valdés' (2002) analysis indicated that *Geitodoris* is more closely related to *Hoplodoris* than it is to *Discodoris*. The present analysis supports this conclusion.

Some general comments about the phylogenetic analyses results now follow. The tree topology was affected by the selection of characters and the choice of outgroups; a situation noted by Ponder and Lindberg when examining Gastropod phylogeny. For example, adding *Discodoris lilacina* to the initial analyses doubled the number of trees but retained the same tree topology and lowered the consistency index. However, in all analyses, the general topology was maintained, that is, only one monophyletic clade resulted that united all species of *Hoplodoris* and *Carminodoris*. *Discodoris* is always positioned at the most ancestral node with *Geitodoris* more closely related to the *Hoplodoris*/*Carminodoris* clade.

Specific details about the taxa in this study are now discussed. In trees resulting from parsimony analyses, *Hoplodoris estrelyado* appears as the most ancestral species. In all trees, *H. grandiflora* appears in a highly derived clade and most closely related to the synonymous species, *H. desmoparypha* and *H. mauritiana*. In the parsimony analysis, the two new species each appear in a highly derived clade. *Hoplodoris bramale* from Costa Rica appears most closely related to *H. nodulosa* from the eastern coast of Australia, while *H. flammea* from Bali appears most closely related to *H. bifurcata*, also found in the tropical Indo-Pacific region.

Thompson's opinion (1975) that Kay and Young's (1969) specimen of *Carminodoris nodulosa* (identified in this study as *Hoplodoris bifurcata*) is not a conspecific of *H. nodulosa* from Australia is also supported by the present analysis. In the parsimony analysis, *H. bifurcata* (= *C. nodulosa* from Hawaii) appears in the sister clade.

Gosliner and Behrens observed that *H. estrelyado* and *H. grandiflora* (= *H. desmoparypha*) are the only two species that have a large, spherical vestibular gland situated on the end of a duct. Parsimony analysis shows *H. estrelyado* as more basally situated to *H. grandiflora*.

Our analyses, along with Valdés' (2002) publication of the phylogeny of the Cryptobranchia allowed us to compare morphological characters to determine common ancestry or independent acquisition of morphological characters. For example, several genera of dorids in clades more basal to *Hoplodoris* have penial hooks (Valdés 2000). These include *Dendrodoris*, *Doriopsilla*, *Onchidoris*, *Calycidoris*, and *Chromodoris*. Within the sister clade of *Hoplodoris*, six genera contain species that have penial hooks: *Alloiodoris*, *Platydoris*, *Gargamella*, *Baptodoris*, *Sclerodoris* and *Nophtodoris*. In the same clade as *Hoplodoris* but more basally situated, some species of *Otinodoris* also have penial hooks. Some genera of even more basally situated clades also have penial hooks (*Onchidoris*, *Calycidoris*, *Chromodoris*, *Alloiodoris*). Thus, it is probable that penial hooks were inherited from a common ancestor and have been lost independently in many taxa within the Cryptobranchia.

Two characters, all radular teeth denticulate and only inner or outer radular teeth denticulate,

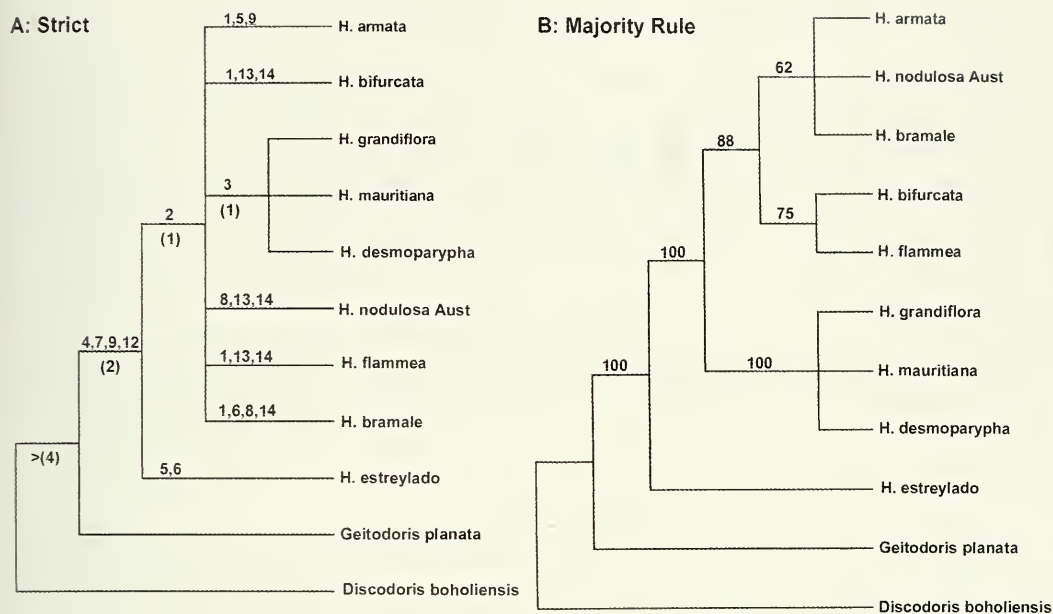


FIGURE 31. Phylogeny of *Hoplodoris/Carminodoris*. — A. Strict consensus tree of 8 most parsimonious trees. Character numbers above the branches are shown with the reversals in bold type. — B. 50% majority rule tree. Numbers shown are the percentage of trees that include that branch. Numbers in parentheses are Bremer support values. — C. Bootstrap results for most parsimonious tree. Numbers above the branches indicate support for that branch. — D. Tree obtained by distance analysis. Numbers indicate branch length.

are present in genera more basal to *Hoplodoris*. *Berthella*, the most basally situated taxon in Valdés' phylogeny of the Cryptobranchia (2002) has all radular teeth denticulate as does the clade with *Actinocyclus*, *Cadlina* and *Chromodoris*. The basal clade containing *Calycidoris* and *Onchidoris* has denticulate inner radular teeth. The clade containing *Goslineria* and *Pharodoris* has denticulate outer radular teeth. Thus it appears that the characters of denticulate and partially denticulate radular teeth were inherited by a common ancestor.

Two characters, an accessory gland with hard structures (spines) and vaginal hooks are not present in any Discodorididae genera basal to *Hoplodoris*. Only in the closest clade to *Hoplodoris*, are these characters present in some species. *Asteronotus*, *Jorunna* and *Nophodoris*, have species with an accessory gland and *Platyodoris*, *Gargamella* and *Baptodoris* have vaginal hooks. It appears that these characters were independently acquired.

SUMMARY

The results from this study indicate that the genus *Carminodoris* Bergh, 1889 is a junior synonym of *Hoplodoris* Bergh, 1880. There are few morphological characters that can be used to justify two distinct genera. It is possible that molecular characters would shed more light on these species and would allow further testing of the species trees by comparison with the gene trees.

Carminodoris nodulosa from Hawaii and *C. bifurcata* from Okinawa appear to be the same species and should be called *Hoplodoris bifurcata* (Baba, 1993). *Hoplodoris desmoparypha* Bergh, 1880, *Carminodoris mauritiana* Bergh, 1880 and *C. grandiflora* (Pease, 1860) are conspecific and should be named *Hoplodoris grandiflora* (Pease, 1860).

Hoplodoris nodulosa (Angas, 1864) and *H. novaezealandiae* (Bergh, 1904) appear to be conspecific.

Hoplodoris nodulosa (Angas, 1864) and *Hoplodoris estrelyado* Gosliner and Behrens, 1998 should be retained as valid species.

Carminodoris armata Baba, 1993 is a synonym of *Hoplodoris armata*.

There are two new species to add to the genus *Hoplodoris*: *Hoplodoris flammea* and *Hoplodoris bramale*. Thus, there are seven valid species in the genus *Hoplodoris*: *H. armata*, *H. bifurcata*, *H. bramale*, *H. estrelyado*, *H. flammea*, *H. grandiflora*, and *H. nodulosa*.

Although the genus *Discodoris* is a closely related taxon, the genus *Geitodoris* is more closely related to *Hoplodoris*.

Important diagnostic morphological characters of *Hoplodoris* that have been inherited from a common ancestor include penial hooks and denticulate radular teeth. Newly acquired morphological characters of *Hoplodoris* species include an accessory gland with a spine and vaginal armament.

ACKNOWLEDGMENTS

Thanks are due to the collectors of these relatively uncommon species of Discodorididae, in particular to Dr Robert Bolland, Larry Sharon, Henry Chaney, Gwen Cornfield, Darryl Takaoka, Mike Miller, Yolanda Camacho-García and David Butvill. Dr Bill Rudman and Ian Loch at the Australian Museum in Sydney kindly loaned the specimens of *Hoplodoris nodulosa* for examination. Many thanks to Lina Daddow of the University of Queensland who took many of the SEM photos of the radulae and reproductive armament. Funding was provided by the following organizations: The National Science Foundation through PEET grant DEB 99-78155 to TMG and The Australian Federation of University Women through the Freda Bage Fellowship to SJF.

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